THE SYSTEMATICS, ECOLOGY AND PHYSIOLOGY OF NEW ZEALAND LANDHOPPERS (CRUSTACEA: AMPHIPODA: TALITRIDAE).

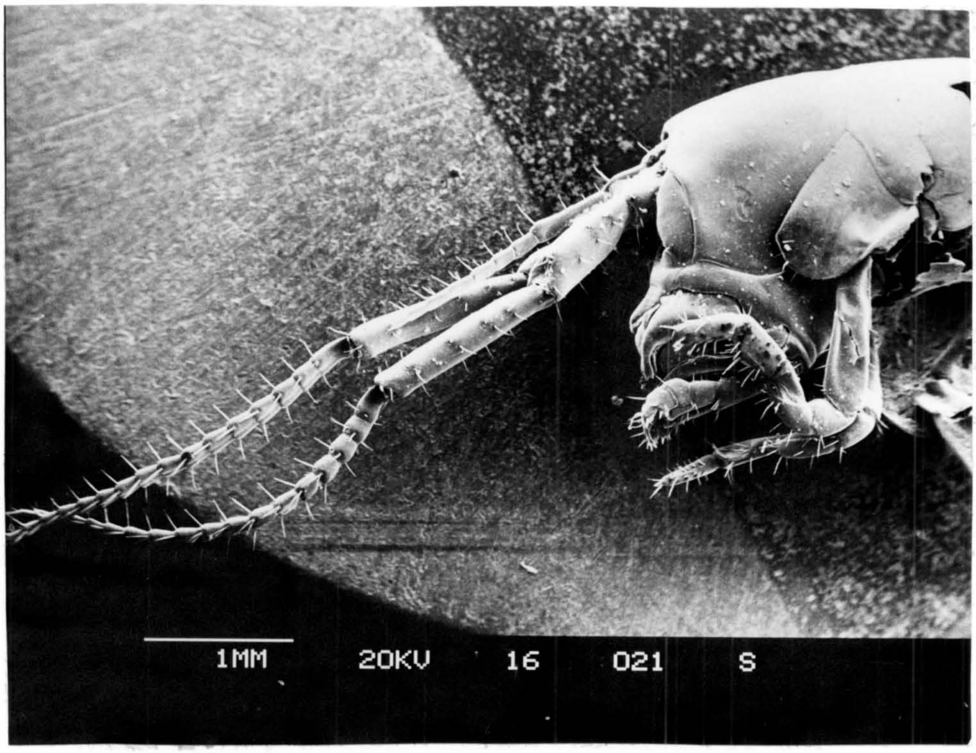
PART I. Systematics and Phylogeny.

A thesis
submitted for the Degree of
Doctor of Philosophy in Zoology
in the University of Canterbury

by

Kelvin Winston Duncan.

University of Canterbury
1984



Frontispiece. SEM of the lateral aspect of the anterior part of *Makawe hurleyi*.

CONTENTS

FIGURES

ABBREVIATIONS USED IN THE FIGURES

A1	Antenna 1
A2	Antenna 2
C	Coxae
D	Distribution
E	Epimeral plates
G	Gill(s)
Gn1	Gnathopod 1
Gn1p	Gnathopod 1 propod
Gn2	Gnathopod 2
Gn2p	Gnathopod 2 propod
L	Lower lip
Mn	Mandible
Mx1	Maxilla 1
Mx2	Maxilla 2
O	Oostegites
P	Penal organs
P1	Pleopod 1
P2	Pleopod 2
P3	Pleopod 3
Pd	Pigmenatation dorsal aspect
Pl	Pigmentation lateral aspect
Pr1	Peraeopod 1
Pr2	Peraeopod 2
Pr3	Peraeopod 3
Pr4	Peraeopod 4

Pr5	Peraeopod 5
S	Side plates
T	Telson
Ul	Upper lip
Ul	Uropod 1
U2	Uropod 2
U3	Uropod 3

If 'f' is appended it indicates female.

If 'm' is appended it indicates male.

If 'l' is appended it indicates left side.

If 'r' is appended it indicates right side.

ACKNOWLEDGMENTS

I wish to thank the Directors and Staff of the following institutions for their hospitality during the periods I worked with them: the Otago, Canterbury and Auckland Museums, the National Museum, the D.S.I.R. Entomology Division, the British Museum (Natural History), and the B.P.Bishop Museum.

Many people are due special thanks for stimulating discussions or help at crucial periods. They include: Dr F.Climo, Dr T.Crosby, Dr R.R.Forster, Dr D.Hurley, Professor G.A.Knox, Mr A.Saville, and Mr K.A.J.Wise.

My wife sustained me during a difficult period and provided me with valuable field assistance.

Mrs K.Card, the University of Canterbury SEM technician, gave unstintingly of her time and effort as we worked together on a temperamental old SEM machine.

Finally, I gratefully acknowledge the great debt I owe my Supervisor, Professor W.C.Clark, whose kindnesses and stimulus over the years are greatly appreciated.

SUMMARY

In Part I of this work the systematics of the New Zealand terrestrial talitrids (landhoppers) are considered and a phylogenetic scheme is presented. Characters used in the determination of taxa and phylogenies include the usual morphological ones, plus stereoscan electron microscopy of the cuticle and body pigmentation pattern.

A number of new species and three new genera are described including: Kanikania (new genus) motuensis (new species), Makawe (new genus) hurleyi, M.waihekensis (new species), M.otamatuakeke (new species), Tara (new genus) egmontensis (new species), T.hauturu (new species), Waematau (new genus) triregis (new species), H.reinga (new species), H.kaitaia (new species), H.unuwhao (new species), H.espiratus (new species), Parorchestia ihurawao (new species), P.longicornis (new species), and Talorchestia aotearoa (new species).

Some previously described species are considered. In particular, Parorchestia sylvicola is shown to be a valid species which is abundant in Northland; P.lesliensis is an upland form with a sporadic distribution throughout the east coast of the South Island and the southern region of the North Island; and P.tenuis is a variable species widespread throughout New Zealand, tending to an upland and inland distribution, but largely absent from the east

coast of the South Island. Further study may prove this latter species to be a species swarm.

Two subspecies of Talorchestia patersoni are shown to exist, one on Snares Island, and the other on Stewart Island and the south-eastern coastal region of the South Island extending northward as far as Oamaru. These subspecies may warrant species status upon further investigation. T.aotearoa is widespread throughout both main islands largely wherever T.patersoni is absent. Thus it is the vicariant sister species to T.patersoni which is the plesiomorphic form. These two species are the only known terrestrial species of Talorchestia, and it is considered that they form the plesiomorphic sister group of the Talitroides-Talitrus assemblage which is absent from New Zealand, but which is present on the other major remnants of Gondwana with the possible exception of South America.

The moderately apomorphic form Talitroides topitotum is a tramp adventive species from India which previously was thought to be an endemic species, Talitrus sylvaticus. It lives in man-made habitats or habitats profoundly affected by man or the animals he has introduced. It is particularly common in Northland, and in the northern urban areas such as Auckland, Hamilton and Wellington. Its success is probably due to two factors: its larger brood size which gives it a high biotic potential, and its resistance to the whitey disease which it brought with it into New Zealand and which is now devastating the native landhoppers.

The vast majority of the landhoppers are thought to have come from only two incursions from the supralittoral or littoral into the terrestrial environment: the Talorchestia-Talitrus-Talitroides assemblage, and the Makawe-Parorchestia assemblage. The differentiation of these two assemblages was already present in the supralittoral. Local origin from supralittoral species on isolated islands, which has been proposed as the mode of origin of the Makawe-Parorchestia assemblage, is probably not possible because it involves sympatric speciation in the face of massive gene flow. Landhoppers on isolated islands, therefore, arrived by dispersal, - either long-ranged or island hopping - or they originated by vicariance or by 'local-neighbour' allopatric speciation and subsequent short-ranged dispersal.

The absence of landhoppers from Laurasia is thought to be due to their vicariant origin in Gondwana, while their absence from South America may be due to competitive exclusion by the hybrid fauna resulting from the biota swap that occurred in the Americas during the Permian. There is, however, an unsubstantiated record of a native landhopper in Chilean rainforests.

In contrast to some other Gondwana fragments, New Zealand has been an active region for landhopper speciation because of its active fold mountain belts. The major phylogenetic events within New Zealand may be associated with major geological events such as: the break-up of Gondwana, the Kaikoura Orogeny, the formation and history of the North Island obducted ophiolites, and the various marine transgressions and regressions which have successively isolated certain parts of the country as islands, or rejoined previously isolated islands to the main land mass.

The major phylogenetic mechanisms have been neoteny and 'reductionism' toward a simpler, less spiny and more delicate body form with less pronounced sexual dimorphism. The robust plesiomorphic body form of the ancestoral supralittoral species is seen as an adaptation to the physical rigours of the supralittoral environment. In contrast, the terrestrial environment is much less demanding physically and allows the development of a smaller and more delicate body form.

The biogeography of the New Zealand landhoppers can be explained by a vicariance model, but such a model seems incomplete because sister groups are not always present, the ranges of many species overlap considerably, and an evolutionary 'trail' of species often occurs from the supralittoral to the fully terrestrial condition. These features can be explained by a form of anagenic evolution involving local dispersal and niche partitioning called 'gressive' evolution which occurs without speciation or the formation of sister groups, but which does result in the formation of apomorphic states from plesiomorphic ones. The mechanism of gressive evolution is thought to involve niche partitioning of two species, which evolved allopatrically initially, but became sympatric by dispersal, and which now occupy more or less the same point on a gradient leading from the supralittoral to the fully terrestrial. Competitive exclusion would result in one species, probably the weaker competitor, becoming more terrestrial, while the other stayed as it was or became slightly less terrestrial. More than likely their ranges would continue to overlap considerably even after competitive exclusion had been operating for some time.

Taxa and area cladograms are given for each of the indigenous genera in New Zealand, and a key to the New Zealand species is included.

INTRODUCTION

The terrestrial talitrid amphipods, or landhoppers, are important members of the terrestrial cryptozoa in New Zealand native forests and grassland litter (Grimmett, 1925; Hurley, 1959, 1968; Stout, 1973; Duncan, 1969, 1981). They can be very abundant with densities of up to 10000 m^{-2} in daytime refugia in particularly suitable sites (Duncan, 1981). Their nocturnal foraging density, however would be much less than this because at dusk they become active and disperse from their refugia.

They are also important in Australia where they are found in mesic sclerophyll and rainforest litter (Sayce, 1909; Campbell and Gray, 1942; Clark, 1954; Sandell, 1977, Friend and Richardson, 1977; Friend, 1980), although they do not appear to occupy as wide a range of habitats as in New Zealand.

Their distribution is of particular interest. In general, they are found in tropical and southern temperate and subantarctic regions (Hurley, 1968). Non-adventive species are absent from northern temperate regions especially North America and most of Eurasia. Their natural distribution appears to include New Zealand, the Pacific Islands, Australia, South Africa, Madagascar, India, Ceylon, the major islands of the Indian Ocean, Burma, Singapore, Indonesia, the Philippines, Japan, the Azores, Madeira, Canary Islands, and the Mauritius Islands (Hurley, 1968). Hurley noted additional records from Jamaica, Haiti, and Panama, while Friend

(1980) cited an endemic species from Mexico found by E.L.Bousfield. However, Hurley (1975) considered his American records to be adventive. Dr Rene Corrubias has also found a landhopper in great numbers in Chile (pers.comm.) although this has yet to be identified.

Within the Indo-Pacific area there have been wide-spread introductions of adventive species. Talitroides topitotum, in particular, is widely dispersed throughout Hawaii (Bousfield and Howarth, 1976), Australia and New Zealand. Presumably, this tramp landhopper of Indian origin has been widely spread by human agencies. Adventive landhoppers are also found in the Americas and Eurasia, where they may become locally abundant (Vader, 1972; Alfonso, 1977; Bowman, 1977; De Castro and Pereira, 1978; Bierbaum, 1980; Richardson, 1980; Friend, 1980; earlier references in Hurley, 1959, 1968, and 1975). Their wide distribution possibly came about last century when Wardian cases were widely used to transport live plants. These cases would have kept soil flora and fauna alive just as well as the plants for which they were intended.

On the basis of their similarity to supralittoral species, it has been proposed by many workers that landhoppers originated from supralittoral ancestors (Bulycheva, 1957; Hurley, 1959, 1968; Bousfield, 1968; Wildish, 1979). Supralittoral talitrids are common on the shores of all major land areas between 60^{o} north and south (Bulycheva, 1957). Hurley (1975) suggested on the basis of their present-day distribution but excluding records from the U.S.A., the Canary, and Azores Islands where it is assumed that introduction from southern hemisphere sources took place, that the '*Talitrus*' group originated in continental Gondwana while most species of terrestrial '*Orchestia*' originated from littoral *Orchestia* in their immediate vicinity. In view of their absence from South America, Hurley considered that they evolved after South America had broken off, but before the rest of Gondwana had broken up and dispersed. Their absence from South America has not yet been confirmed, however, in view of the record from Chile reported above. Friend (1980) suggested that the Talitroidea radiated in Gondwana and that supralittoral talitrids were not present in Laurasian continents until the late Tertiary.

Their virtual absence (except for a few introduced species) from North America and Europe means that knowledge about the group is very rudimentary and sparse. The few studies on their ecology and physiology in New Zealand have been conducted by Grimmett (1925) and Duncan (1968, 1981).

The present study was aimed at a survey of the ecological physiology of the group, but before this could be completed a study of their systematics had to be made. Thus Part I of this work deals with the taxonomy and phylogeny of the New Zealand talitrids while Part II deals with their ecology, behaviour, and physiology.

The first terrestrial amphipods known to science from New Zealand were Orchestia tenuis and O.sylvicola which were described by Dana (1852, 1853 and 1855) from specimens collected in Northland. There was to be much controversy during the next 130 years about these two species. Chilton (1909) added substantially to our knowledge of the southern forms when he described four new species from the subantarctic islands and Stewart Island. Stephensen (1938) described two forms of what appeared to be a new species of Parorchestia: P.stewarti f.brevirostris and P.stewarti f.longicornis, as well as Talorchestia patersoni. In a series of important revisions, Hurley (1955, 1957) added four new species in the genus Orchestia. He reduced the number of terrestrial genera in New Zealand to two by referring Parorchestia to Orchestia on the grounds of insufficient separation, and referring Talorchestia patersoni to Orchestia. He also attempted to clear up the considerable confusion that surrounded the 'tenuis'-type by merging stewarti, sylvicola and tenuis into O.tenuis. The final species before the present work was added by Bousfield (1964) who described Parorchestia campbelliana from Campbell Island.

Thus about 11 truly terrestrial species were known from the New Zealand region, although Bousfield (1964) considered this to be only a small portion of a comparatively rich landhopper fauna.

The reason why so few landhoppers were known from New Zealand, in spite of the numerous publications on the group, was because most previous studies relied on the morphological characteristics which had been traditionally applied to marine and supralittoral species of Amphipoda. Most of the workers publishing on landhoppers had a marine background, and their expectations were that traditional methods would resolve the taxonomic difficulties in this group which, after all, are very closely related to supralittoral and intertidal amphipods.

Unfortunately, these expectations have not been realised. In fact, the use of traditional techniques lead to such confusion that Thomson (1881) thought that there was only one species in New Zealand: *Orchestia sylvicola*, which he considered to have a very variable coloration and morphology. And in the higher taxonomy Hurley (1957) was forced to 'lump' all *Orchestia*-type species into the one genus: *Orchestia*, because he was unable to find criteria which would reliably separate subgroups.

The realisation that there were many more landhopper species present in New Zealand than had been described came to me during my physiological and ecological studies on living amphipods. The range of behaviours, body patterns and morphologies I observed during the course of these studies - which generally entailed very close examination of a great number of live specimens - forced me to the conclusion that there were numerous new species of relatively constant morphology. Thus of necessity for my ecophysiological studies, I embarked on a study of New Zealand landhopper systematics, developing the necessary concepts and techniques as the study progressed. This work has resulted in a complete review of the New Zealand landhopper fauna with the description of four new genera and 14 new species thus increasing to 24 the number of terrestrial talitrids in the New Zealand region (as defined by Cochrane, 1973).

According to Mayr (1969) taxonomy has two principal aims: the description and identification of species and the elucidation of the phylogenetic relationships between groups of organisms. The former is often referred to as 'alpha' taxonomy while the latter is 'beta' taxonomy. In addition to describing new species and establishing the ranges of known species, I have attempted to unravel the phylogenetic relationships in the New Zealand terrestrial talitrids - beta taxonomy - and thus gain a better insight into the important processes and factors involved in their conquest of the terrestrial environment.

METHODS

Specimens were collected using an entomological aspirator (pooter) of a design (Figure 1) which could be operated by one hand allowing the other hand to move litter and soil aside. The body of the pooter is made of wide diameter polythene tubing and the narrow tubes are also of polythene so that the whole is as robust as possible. The user is protected by a double filter system where one filter is bolting silk and the other tissue paper. In recent years Dr T.K.Crosby, of the Entomology Division of the New Zealand Department of Scientific and Industrial Research, introduced me to their method of collecting using pyrethrum-based insecticidal sprays in a pressurized can. This is very efficient, but I had to discontinue the use of a pooter because of the fumes. Forceps tend to crush amphipods so instead a car vacuum cleaner ('Anex' brand, Hong Kong) was used with a body pack of 2, 6V dry cells wired in series. This equipment was still very light and portable and it was very efficient for the collection of landhoppers, as well as other cryptozoa, when used in conjunction with a spray can of insecticide.

In older collections I had noticed severe deterioration of specimens on prolonged storage. In the National Museum of New Zealand for instance, specimens collected between 1940 and 1950 have a semi-macerated appearance. And the Canterbury Museum, many of the specimens collected by Chilton early this century have been totally destroyed. The damaged material has a blackish-brown appearance and is soft and macerated with little visible form. Dingerkus (1982)

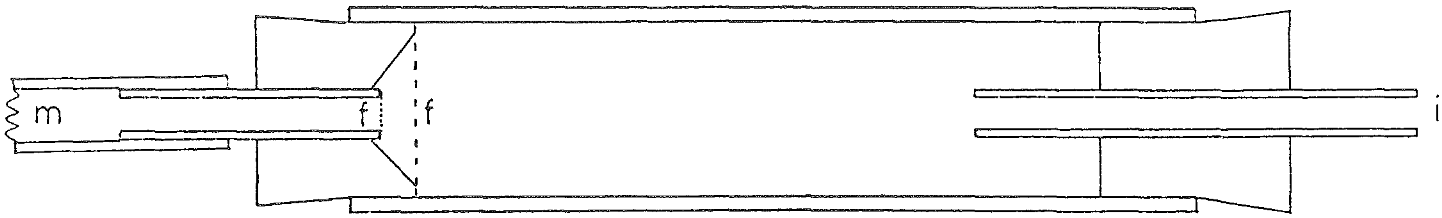


Figure 1. Entomological aspirator used for collecting landhoppers. i, inlet; f, double filter; m, mouth tube made from 600 mm of flexible polythene tubing.

reported the same problem in the storage of fatty fish. The storage medium in which the damaged material was contained had a pH of 5.5 when tested with multiranged pH paper, and it often gave off a peculiar odour. Hydrometer tests showed that the storage medium had not become diluted appreciably. A possible cause of this phenomenon is autolysis due to breakdown of triglycerides to fatty acids and glycerol. The free fatty acids thus liberated would decalcify and eventually disarticulate the specimens. Any glycerol present in the storage medium may well hasten this process by softening the body. Further breakdown could be responsible for the release of gaseous products which give the characteristic bad odour noted in tubes containing damaged material.

To prevent similar damage to my own specimens a small quantity of chalk or coral was placed with the specimen(s) in each tube, and the preservative (70% alcohol with 1% glycerol - Wagstaffe and Fidler, 1958) was changed each year for three years.

Each tube was given a catalogue number when processed, written on an internal label and on a colour-coded disc which fitted on the lid of the tube and held in place by Parafilm M (American Can Co.). The Parafilm also prevented evaporation. The colour codes of the discs were: red for types, green for important material and white for ordinary material.

The catalogue was maintained on an Apple II+ microcomputer using an Applesoft Basic program called MIDAS (Multiple Indexed Disc Accessing System). MIDAS allows disk text files to be created with records of up to 30 fields each. Input is prompted with the name of the field and the record number. Records may be added to, or deleted from, existing files. Global replaces and searches are possible. The file may be printed in alphabetic order based on any field and column(s); partial listing is possible, and printing can be in a wide variety of forms. User-defined macros are also available, which are very useful when the same species names are being entered repeatedly; instead of having to type the whole name in, only the special function key associated with that name need be pressed. There are many other features in MIDAS which make it a very useful tool for museum-type catalogues.

Photomicrographs were taken using a photo-extension tube on a Wilde M5A stereoscopic microscope with an Olympus OM 10 body attached, thus obtaining the great advantage of automatic exposure. The Wilde quartz-halogen, 'through-the-lens' light source was a failure for this set-up since some of the light reflected back up the microscope to the camera instead of all being incident on the specimen. So standard tungsten lights were used which gave good results with colour film of the correct colour temperature rating. Photography was mainly used to record the specimen's colour pattern since this was found to be an important, if unfortunately transient, character which enabled the easy recognition of species which were otherwise difficult to identify. For the sake of publication, drawings were made from these photographs as well as directly from actual specimens.

Dissection followed the methods given by Barnard (1969), and was carried out while the specimen was pinned by a minuten entomological pin and held under alcohol on a bed of wax to which carbon black (i.e., lamp black) had been added while molten.

Early in the study I used euparal as the mounting medium, but I later changed to P.V.A for routine work when the advantages of this medium were more fully appreciated. I used Salmon's Type 2A (Gatenby and Beams, 1950) to which a little lignin pink, sufficient to give the solution a faint pinkness, had been added. This dye stains chitin and renders cuticular parts even more visible in an already excellent mounting medium.

Morphometric analyses were carried out on the following measurements: body length (antenna 1 base to telson); antenna 1 length; antenna 1 flagellum length and number of flagellar segments; antenna 2 length; antenna 2 flagellum length and number of flagellar segments; gnathopod 1 propod length, width and palmar angle; gnathopod 2 propod length, width and palmar angle; peraeopod 5 basos width and length; peraeopod 5 propod length; uropod 1 length and outer ramus length. Most of these measurements could be made on the virtual image of an undissected specimen given by a Wilde M5A stereoscopic microscope with a camera lucida attachment. The specimen was held in place by black sand while being examined; I was introduced to this technique by Dr F.Howarth of the B.P.Bishop Museum, Honolulu.

The morphometric data were analysed using analysis of covariance (ANCOVA), applying transformations where necessary to achieve linearity. The ANCOVA program, called REGTEST, was written in FORTRAN IV and run on a Burroughs B6930 computer. Cluster analyses were also tried but the analyses were disappointing because the animals from one population or OTU were not constant in their morphological attributes. A population may consist of small individuals without spines, larger individuals with a few spines, while the few oldest individuals have many spines. Cluster analyses were unable to group these together whereas ANCOVA copes with this situation well, since such a relationship can be expressed as a regression and the characteristics of the regression can be tested for homogeneity very simply. If it were possible to collect enough specimens of the same instar cluster analysis may be worthwhile, but at present ANCOVA is the more powerful technique. To test the reliability of the ANCOVA technique, 30 individuals each of *Makawe hurleyi*, *Parorchestia tenuis* and *Kanikania motuensis* were measured and analysed using ANCOVA. The analysis involved interspecific comparisons of the regressions of the measuremnets of one body part against another for all the body parts measured. The regressions were significantly different at a probability level of less than 0.00001% in all cases.

The surface microstructure of the cuticle - particularly that of abdominal segment 2 and the uropods - was investigated using a Cambridge S 600 stereoscan electron microscope initially, and then, for the latter part of the work, a Cambridge Stereoscan 250 Mark 2. In particular, the distribution and form of the mucus glands discovered by Shyamasundari and Hanumantha Rao (1974) was investigated with SEM (Kessel and Shih, 1976) and histochemical tests using periodic acid-Schiff, alcian blue and safranin O reagents.

TERMINOLOGY

Spination

Current standards in taxonomy make it necessary to indicate the spination of the appendages. A simple terminology is used here which is a modification of that introduced by Barnard and Barnard (1982). It indicates not only the position of the spines in the spine groups on the appendages, but also their number and kind. The distance of the spine groups is expressed as a proportion of the length of the segment on which they occur, working from proximal to distal, and using that line which passes through or close to the base of the spines. Thus for spines on the anterior margin, the measurements are made on a line joining the anteroproximal angle to the anterodistal angle. Posterior margin spines are measured on a line connecting the posteroproximal angle to the posterodistal angle. It is necessary to use separate lines for the anterior and posterior margins since the shape of some segments precludes the use of a single, axial line. The number of spines in a spine group is shown in brackets after the proportionate length measurement for that group. If no number is given in brackets then only 1 spine is present. Where necessary, the spine count is broken into 2 parts: the first part gives the number of large spines in the spine group while the second part gives the number of small spines. Such a partitioning is naturally very subjective and it does not indicate the absolute size of the spines, but it is included where it seemed important to indicate that there is a marked difference in the relative sizes of the spines in a spine group. Thus the spination of the anterior margin of the segment shown in Figure 2 can be expressed as 0.15, 0.28 (2+1), 0.58 (2+1), and 0.93.

Scionate

Many spines on the appendages have a small accessory branch at their distal tip. Charniaux-Legrand (1952) reported these structures, which she termed 'extremite bifide', in the peraeopod spines of Gammarus locusta, Orchestia mediterranea, O.montagui, and

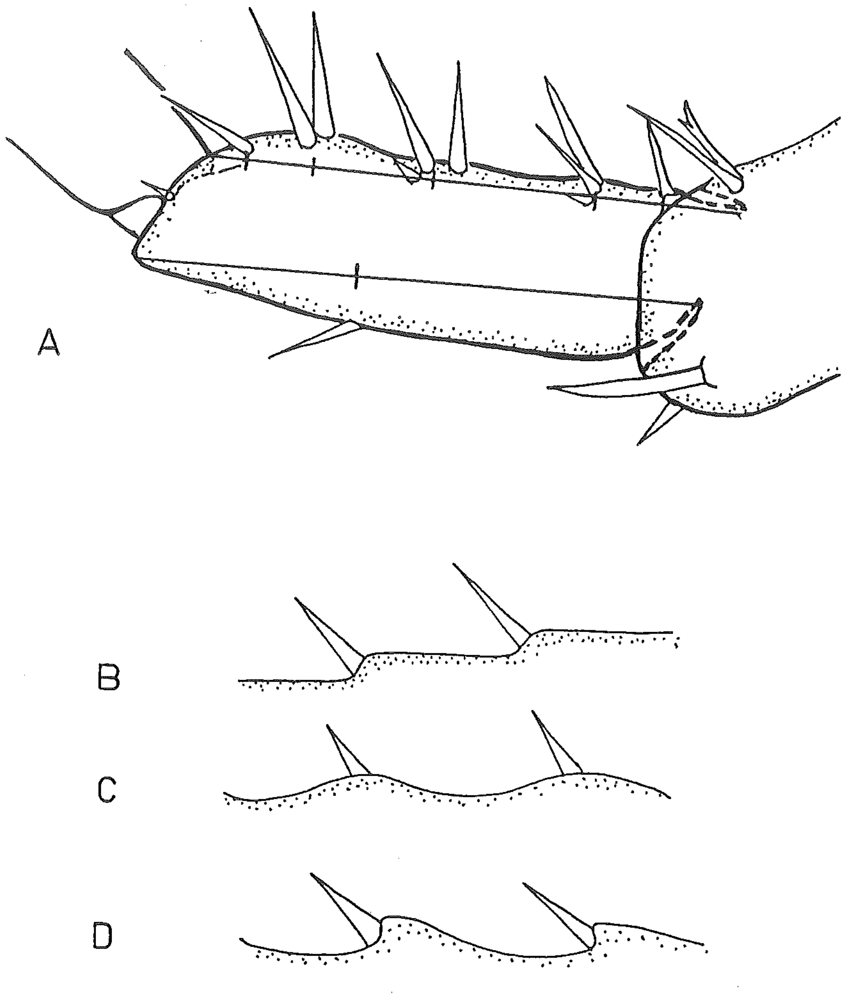


FIGURE 2. Spination indices and morphological features.

O.gammarella. Hurley (1957), Dahl (1973), and Friend (1979) have also reported these 'bifid' spines. They are termed scionate spines in this work. Figure 399 is a stereoscan electron micrograph of a typical scionate spine. The accessory branch is ridged or foliate, and is usually bent away at an angle from the main spine. Presumably, it has a tactile sensory function.

Plinthic ridge

This is the spined ridge present in many species at the base of gnathopod 1, immediately proximal to the beginning of the basos.

Stepped

Immediately distal to the insertion of spines or spine groups on the appendages there is often a sudden narrowing or step. Figure 2b illustrates this.

Scalloped

The margin between spine groups in certain appendage segments may be emarginate or concave. Figure 2c illustrates this. Margins may be both stepped and scalloped as illustrated in Figure 2d.

Abbreviations for sexes and broods

The following symbols are used: M = male, F = female, imm = immature, b = brooding, nb = not brooding, e = eggs at an early stage in their development, m = eggs at a mid-development stage, l = eggs at a late development stage, h = hatched.

Morphological terms and dimensions

Morphological terms used throughout this work generally follow those given by McLaughlin (1980). The dimensions of body parts relative to those of other parts are expressed as proportions.

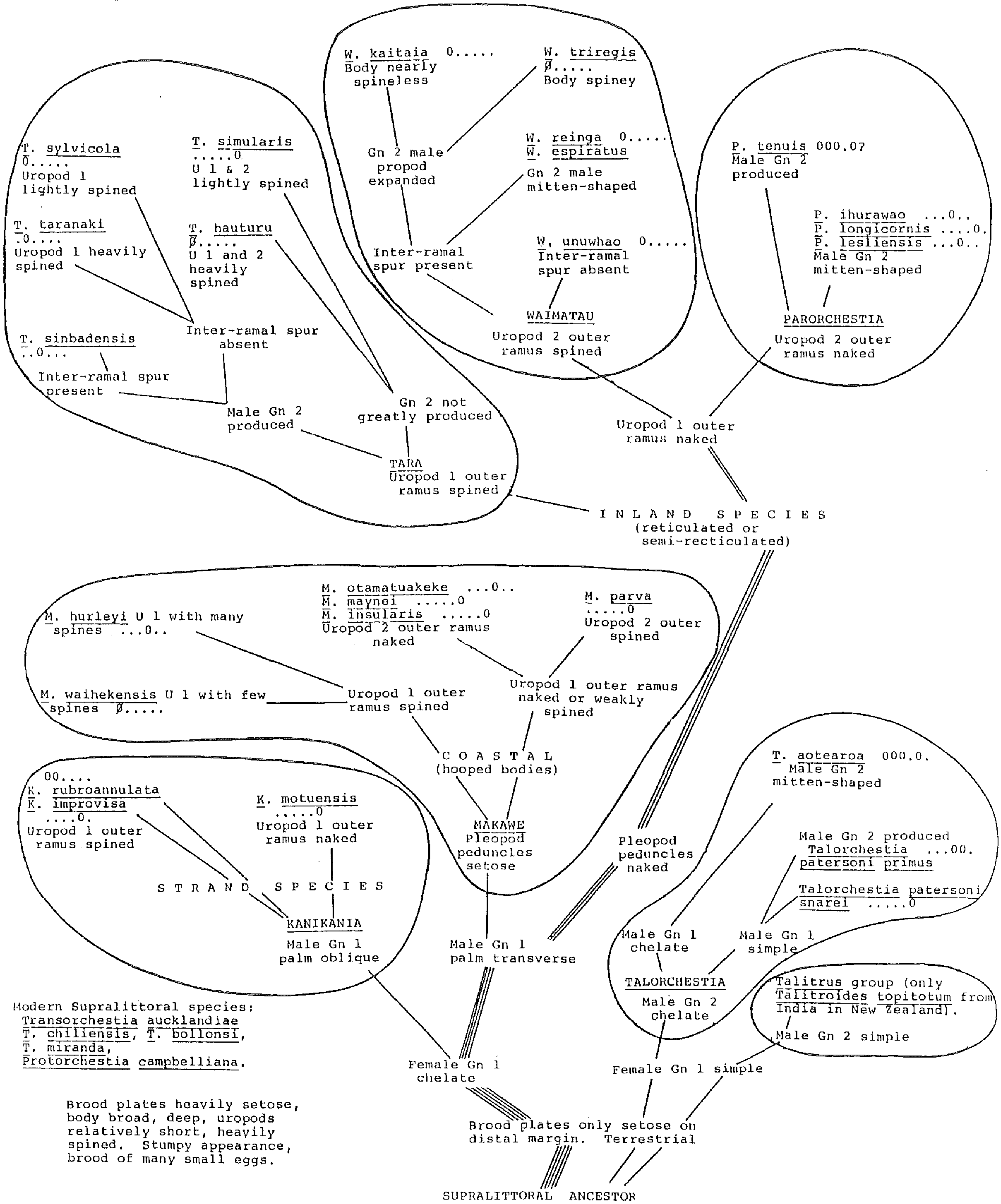


Figure 3. A phylogenetic subdivision of the New Zealand terrestrial Talitridae. _Talitroides topitotum_ is an adventive species and has been included only for completeness. The distribution of each species is shown by symbols indicating: '.' = absent, '0' = present, 'Ø' = present off-shore. The position in each row indicates region, thus: position 1 = Northland, position 2 = rest of North Island, position 3 = west coast South Island, position 4 = east coast South Island, position 5 = Stewart Island, position 6 = subantarctic islands. Thus ....0. indicates presence on Stewart Island.

PHYLOGENETIC CONSIDERATIONS

The aim of systematics should be not only to name new species and to provide a means for identifying known species using hierarchical classificatory systems ('alpha' taxonomy) it should also aim at isolating and identifying natural groups and the evolutionary relationships between these groups (beta taxonomy).

Hurley (1957) considered the taxonomic difficulties in separating the supralittoral members of his '*Orchestia*' group from the more terrestrial members. He maintained that the absence of absolute criteria for separation made it desirable to 'lump' the groups into *Orchestia*, a view he reiterated in 1974. Certainly the separation is not absolute since the landhoppers are very diverse in their terrestrial status. There is a continuum of forms from those which are only slightly terrestrial and which closely resemble their supralittoral relatives, through to thoroughly terrestrial species with many adaptations toward terrestrial life. Yet there is a real difference between the supralittoral and the terrestrial forms even though it is often a matter of degree rather than quantal. Thus Hurley's (1957) solution to the taxonomic difficulties presented by the terrestrial talitrids, whereby he merged all *Orchestia*-like species into *Orchestia*, is not very satisfactory since it does not achieve the aims of beta taxonomy. The genus *Orchestia* as defined by him would thus encompass a great number of forms showing a wide diversity of body form and habit, ranging from the supralittoral to very terrestrial environments.

Bousfield (1982) has proposed a subdivision of the Talitridae which appears to work well in practice, so that the difficulties mentioned by Hurley appear to be overcome. And as well as the formal subdivision Bousfield has provided a very useful informal subdivision of the Family Talitrid based on systematics, ecology and behaviour, into the following groups: (1) palustral talitrids which are semi-aquatic in salt marshes and mangrove swamps, (2) beach fleas which are mainly intertidal and coastal leaf litter, non-substrate modifying talitrids, (3) sandhoppers which are intertidal, substrate modifying talitrids of sandy beaches and (4) landhoppers which are truly terrestrial, non-substrate modifying talitrids. He concludes that since each group contains at least two obviously convergent generic morphotypes, and is therefore polyphyletic, no formal recognition of these four groups is possible. Nevertheless, the subdivision proposed by him has a very great utility.

In an attempt to devise a more satisfactory phylogenetic scheme for the terrestrial species, a fresh analysis of the problem of the phylogeny of the New Zealand '<u>Orchestia</u>' assemblage was made using the well-established evolutionary principles of neoteny and derived states. Neoteny, as defined by De Beer (1951), is the retention of juvenile characters into the mature stage or the development of sexual maturity in the young of a species. Many landhoppers show this kind of evolutionary change, particularly with respect to their gnathopods, uropods and pleopods.

It is assumed that neoteny (which De Beer equates with paedomorphosis) has been a common evolutionary mechanism and has occurred independently in many groups of landhoppers. We can speculate that, as the animals evolved toward the terrestrial condition by becoming smaller and less heavily bodied, carrying during courtship and copulation became more and more difficult. We do not know the copulatory position of many talitrids, but in neither Makawe hurleyi nor Paraorchestia tenuis do the males carry the females during courtship and copulation (Part II). As carrying became redundant so thereby did large male gnathopods. The selection pressure for the reduction of large male gnathopods through neoteny could come about because large gnathopods are cumbersome and require considerable amounts of energy and matter to grow. If they are functionless then their reduction confers advantage. In some groups, Talitrus and Talorchestia for example, the first gnathopod has become completely simple which, therefore, must be regarded as an advanced (apomorphic) feature. Most groups, however, retain a chelate first gnathopod because it performs other functions such as: food manipulation, grasping excuviae during moulting, and manipulating the other individual during copulation.

The other principle applied to sort out the phylogeny is that of derived states and characters (Henning, 1966). The problems of what are derived characters and what are not apparently can be resolved quite easily in landhoppers, because, if it is true they evolved from supra-littoral ancestors, then the supralittoral state or 'morph' is the most plesiomorphic one and the characters shown by terrestrial species which deviate from this state are derived characters. Particular derived states could be detected in species with lost body parts. Species with lost parts were considered to be more highly evolved (apomorphic) than species with that part (or parts) still present. For example, species with naked outer rami on their uropods are considered to be more advanced than those with spines present. This phenomenon is termed reduction in this work following De Beer (1958), and the concept of the reductionist origins of derived characters, turned out to be a powerful approach in the reconstruction of landhopper phylogeny.

The key morphological changes in the New Zealand landhoppers seem to have been:

- the reduction in the spination on the oostegites (brood plates);
- the loss of setae on the peduncles of the pleopods;
- the loss of spination on the outer ramus of uropod 1;
- followed by the loss of spination on the inner ramus of uropod 2.

These primary events were followed by a number of reductionist events of lesser or secondary phylogenetic significance (though, no doubt, of great ecological and physiological importance), such as reduction of pleopods, and reduction of gnathopods. These secondary events seem to have occurred independently in a number of landhopper groups occupying other regions as well as New Zealand. Thus parallel evolution has apparently occurred widely in the evolution of landhoppers because of common selection pressures and the canalised evolutionary potential of landhoppers due to their monophyletic ancestry.

The phylogenetic analysis is presented in schematic form in Figure 3 which suggests the following points about the evolution of the landhoppers in New Zealand:

(1) There are no *Talitrus*-type species endemic to New Zealand. If the landhoppers did originate in Gondwana before its break-up then the *Talitrus* group evolved after New Zealand became isolated from the Australian land mass between 60 and 105 million years ago (Stevens, 1980). The *Talitrus* group are the dominant species in Australia although '*Orchestia*'-type species are present.

(2) *Talorchestia* has made only a limited incursion towards terrestrialism. The most advanced species in this group are *T.patersoni snaresi* and *T.aotearoa* which are still mainly coastal. Possibly, these terrestrial *Talorchestia* species form the vicariant sister group to the '*Talitrus*' assemblage. The vicariance event was the separation of New Zealand from Gondwana, with the plesiomorphic group becoming isolated on New Zealand while the sister group evolved to the apomorphic *Talitrus* assemblage.

(3) The '*Orchestia*' lineage shows gradations of forms exhibiting increased terrestrialism. The strand species - which are

those inhabiting the strip of land immediately adjacent to the shore, in a community of organisms typified by plant species such as ngaio, Myoporum laetum, and pohutukawa, Metrosideros excelsa - are the most primitive as shown by their spiny bodies. The next group shows advances on the strand group, but is still limited to coastal situations. The most terrestrial species inhabit inland and upland areas. This group shows reduction of both pleopods and secondary sexual characters. Bousfield in the discussion on Hurley's (1968) paper suggested that landhoppers are restricted to areas with a certain salt load in the environment. In a sense this is true for primitive species but fully terrestrial species are not restricted by salt load (Friend, 1980). However, it is obvious that ionic and osmotic relations are important in the evolution of landhoppers to the terrestrial condition and this is further considered in Part II of this work.

(4) In general, the more advanced species are northern in their distribution. There are one or two exceptions, but the majority of southern forms are more primitive both in their ecology and morphology. Two things could account for this. As New Zealand drifted slowly northwards following its isolation from Gondwana, the landhoppers on the main land mass evolved gradually and progressively toward a more terrestrial condition. During this time the southern islands became isolated and they carried with them the forms that had evolved at the time of isolation. Commonly, these species 'left behind' would have been the more primitive coastal forms rather than the more terrestrial inland forms because of the

relative paucity of inland habitats on small islands. Further evolution toward increased terrestrialism would have been limited on these isolated southern islands because they probably lacked large areas of truly terrestrial environments since they were much smaller than the main New Zealand land mass.

Such a view of the landhopper biogeography of these southern islands is not in accord with Macarthur and Wilson's (1967) ideas on island biogeography, but the persistence of primitive forms in New Zealand's southern islands does not fit their theory. Chance dispersal from the mainland, the essential biogeographic 'force' in their theory, could occur, but the predominant east-west drift (Atkinson and Bell, 1973) makes the chance of such dispersal very remote.

Within New Zealand the majority of advanced species are found in Northland. This may be because speciation is more widespread there due to the very active geological processes which have occurred (and are still occurring) in that region (Brothers and Delaloye, 1982). Here populations may have become isolated on temporary islands or seamounts long enough for speciation to occur. And since there have been many seamounts and temporarily isolated islands the fauna is particularly rich in species.

A few of the mainland New Zealand species are widely distributed, but these tend to be found only in mesic areas. In the more arid region of the eastern and central parts of the South

Island, in the rain shadow of the Southern Alps, the predominance of small, weakly sexually dimorphic forms is marked. These species may have a highly skewed sex ratio toward females which is possibly adaptive for the comparatively arid conditions - which may receive less than 560 mm of precipitation per year - in which they live. Small body size would enable them to occupy the more numerous smaller refugia during the droughts to which this area is periodically subjected. Small males may be sexually active if the species does not rely on carrying during courtship and copulation. Makawe hurleyi, which is a dominant species in the drier zone of South Island, shows sexual dimorphism in body size in that the males are smaller, an obvious adaptation for the stressful conditions in which the species lives.

Skewed sex ratios in species living in drier zones may be explained, in part at least, by the very natural tendency of collectors to overlook small specimens. If the species shows sexual dimorphism in body size, then the smaller sex will be under-represented in collections. However, modern collection techniques are not prone to this fault and the sex ratio in some species cannot be due to collector bias. An ecological bias may come about because males may be subjected to higher mortality as they move about in search of females. Rain-shadow species may also have a genetically determined low ratio of males because the attractant pheromones given off by recently moulted mature females (and which sends the males in cultures into a veritable frenzy of activity) can travel further in dry habitats and thus attract males from further abroad. In wet environments the pheromone would not be able to disperse as far on average because it would be removed from the air by precipitation. It is a feature of wet, mesic forests that males are large and common. This is not so in the species inhabiting drier forests.

Within the main New Zealand land mass most speciation appears to have taken place in far northern and in southern regions because the greatest number of species are found in Northland, the Catlins district and Stewart Island.

(5) The species within each genus tend to occupy different regions. It may appear that this is not so for some species from the information given in Figure 3, but the regions are only crudely outlined this figure and a more detailed description would show that they are, in fact, geographically separate. For example, in the figure all the subantarctic islands are merged together as one region, but each island tends to have its own unique landhopper fauna. Closely related landhopper species are almost always allopatric although sympatry of distantly related species is common throughout New Zealand with 2, 3 or even more species living together in most localities.

Independent evidence for the correctness of the scheme outlined in Figure 3, at least for its broad outlines, is given by the body pigmentation pattern. Although these patterns are not known for all species sufficient are known to show that advanced species (like

Parorchestia) are reticulated, less advanced species are semi-reticulated or spotted, while the more primitive strand/coastal species, such a *Kanikania rubroannulata*, are striped or hooped. Pigmentation was not used in constructing the phylogeny so it is of considerable importance that a phylogeny based on this character agrees in broad outlines with that based on reductionism.

The homologies on which this reconstruction is based satisfies Patterson's (1980) tests in that they are all similar, they do occur in a single individual (at the stem), and they are congruent. But without doubt there has been considerable parallelism in the evolution of landhoppers. Thus world-wide 'homologies' (in the sense of similarities) cannot be used for phylogenies or classifications without a considerable knowledge of the regional phylogenies subsumed in the world-wide grouping. *Parorchestia*, for instance is almost certainly an endemic genus with no close relatives beyond the New Zealand region. Any similarity to other groups in other regions is likely to be due to parallelism and not direct homology.

Most of derived characters seen in landhoppers came about because of the processes whereby the bodies of terrestrial species became lighter, more delicate and smaller once freed from the rigours of the supralittoral environment. Large body size and robustness probably confers advantage in the littoral and supralittoral because the animals which live there are subjected to much force and disturbance from tidal and storm-driven beach sorting processes. Terrestrial environments, on the other hand, are far less subject to physical disturbances. Here the natural advantage of small body size (MacMahon and Fowler, 1982) would result in an evolution toward delicate, small-bodied species with a simpler spination and reduced sexual dimorphism. As noted earlier, this may have come about by neotenous processes. Such tendencies would occur no matter which region on the globe was occupied since similar causal factors would be present in all mesic terrestrial environments. Thus all terrestrial landhoppers would be expected to show parallelism in their evolution no matter how isolated the regions are from each other and how little interchange there has been between the talitrid faunas of these regions. Derived characters, therefore, must be interpreted with care and should not be used to link apomorphic groups across regions. For instance, the fact that some groups in both New Zealand and Australia have reduced pleopods is no justification for linking these groups into one higher assemblage, since pleopod reduction, an apomorphic characteristic, probably has occurred independently in both places as an adaptive response to common environmental demands in separate groups belonging to the same broad generalized track (Croizat et al, 1974) and showing similar evolutionary propensities or 'unique inside parallelism' (Brundin, 1981).

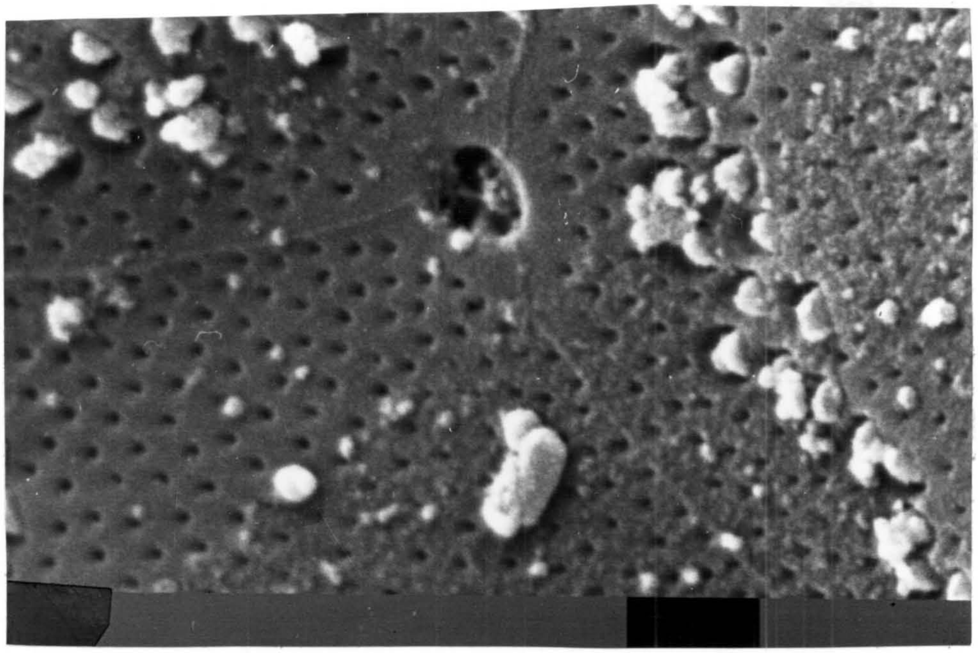


FIGURE 4. Cuticular structures in Transorchestia chiliensis. Note the double row of mesopores arranged as an arc set back from the posterior margin of the cuticular polygon boundary, a large macropore opens at the junction of the polygons, micropores are present and the polygon boundaries marked by a definite linear structure. The scale bar represents 1 micrometre. The 'blobs' are mucoprotein material.

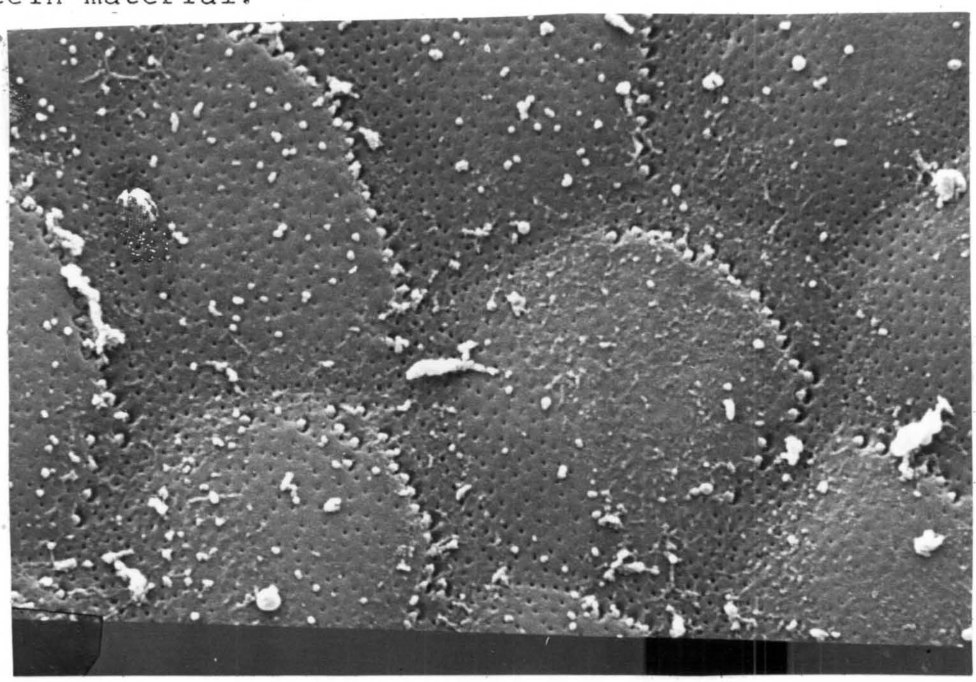


FIGURE 5. Cuticular structures in Talorchestia quoyana. Mesopores are arranged in arcs set back from the posterior margins of the cuticular polygons. A few mesopores are scattered over the surface of the polygons. The scale bar represents 4 micrometres.

SYSTEMATIC SECTION

Kanikania new genus

Parochestia Chilton, 1909:641; Shoemaker, 1935:66; Stephensen, 1935:13; Stephensen, 1938:251-252.

Diagnosis.

Small, plesiomorphic landhoppers, characterised by the marked chelate development of gnathopod 1 in both sexes, and the mitten-shaped gnathopod 2 in both sexes. Antennae 2 with fine setae. Only weakly sexually dimorphic. Pleopods short, broad, may be reduced or vestigial. Uropod 1 outer ramus weakly spined or not at all.

Etymology: from the Maori for 'dance'; a translation of orchestia.

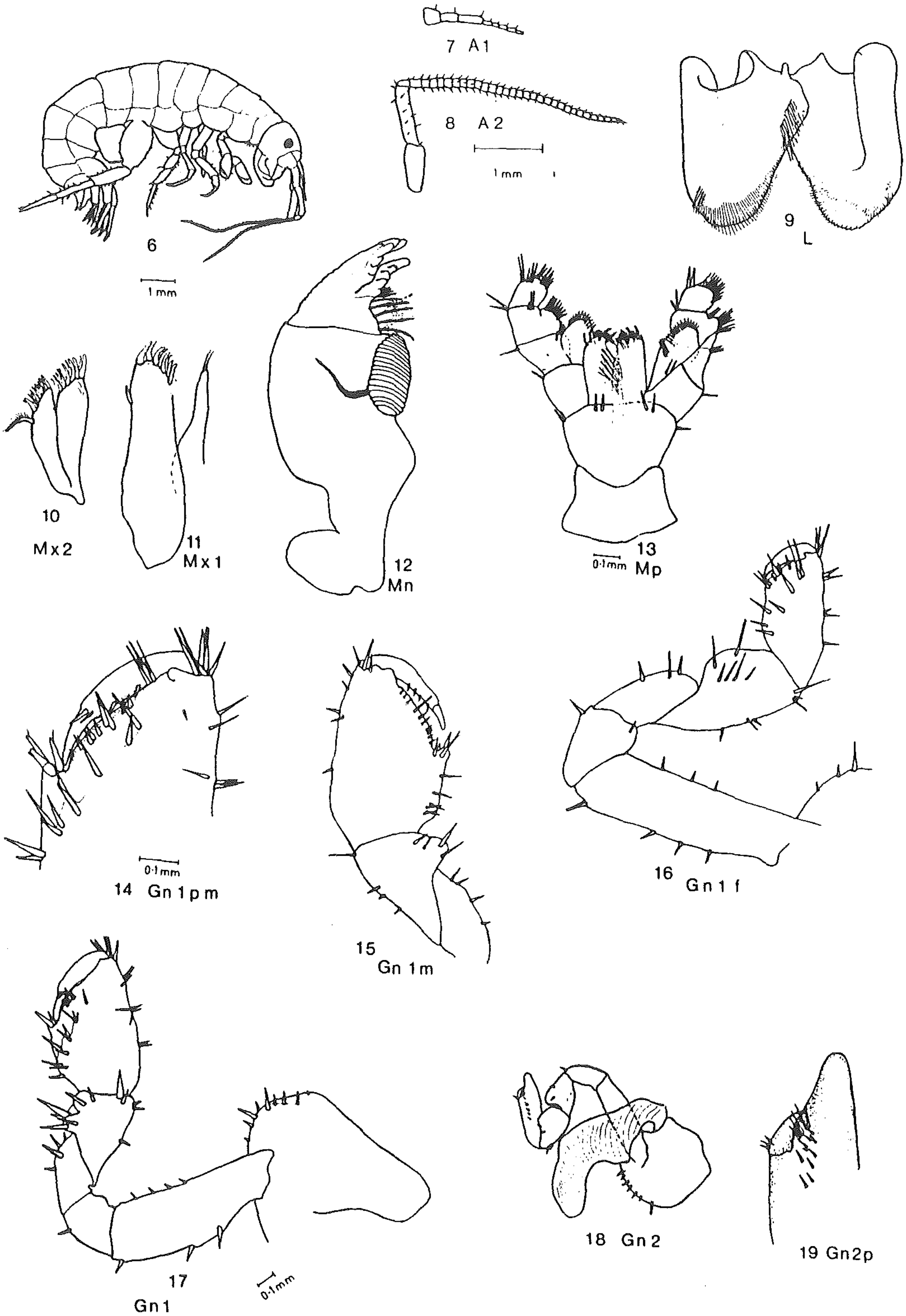
Type species: *Parorchestia improvisa* (Chilton, 1909).

Other species: *K.rubroannulata* (Hurley, 1957), *K.motuensis* new species.

Remarks

This genus is clearly distinguished from other talitrid groups by the pronounced development of the propod and dactyl in gnathopod 1. Some feminized species, such as *Makawe hurleyi*, may be related to it, but most of these species can be excluded on one ground or another. In the case of *M.hurleyi* the presence of strong spination on the outer ramus of uropod 1 indicates that it is not as closely related as might otherwise be suspected.

The members of this genus have an interesting ecology. They live in marine fringe forests in soil which may be quite saline. I have termed these soil types 'high tonicity' or 'high conductivity' soils, because of the salt load present from sea spray or enlarged first gnathopods which seem to be used for digging in the loose, friable, well-drained soil typical of these habitats. Unlike most bush hoppers, during dry periods they are able to escape downwards in friable soils to moist microenvironments. The tonicity of these soils during dry periods is high: I measured on soil on the Whangaparoa Peninsula which had soil water with an osmotic pressure equivalent to 130% that of seawater.



FIGURES 6-19. Kanikania improvisa. 6, lateral aspect. 7, antenna 1. 8, antenna 2. 9, upper lip. 10, maxilla 1. 11, maxilla 2. 12, mandible. 13, maxilliped. 14, gnathopod 1 dactyl and palm. 15, gnathopod 1 propod and dactyl. 16, gnathopod 1 female. 17, gnathopod 1 male. 18, gnathopod 2 male. 19, gnathopod 2 male propod and dactyl.

Kanikania improvisa (Chilton, 1909).

Figures 6 to 30, Figure 62.

Parochestia improvisa Chilton, 1909:641, Figure 10; Shoemaker, 1935:13; *Orchestia improvisa* Hurley, 1957:183-185.

Types:

Holotype: Snares Island. Coll. G.R. Mariner, Canterbury Museum, Chilton Collection, Slides A1-A6. Allotype: tube containing an intact female.

Other material used to supplement descriptions was collected by P.M.Johns from Snares Island, opposite Mollymawk Islet, by beating *Poa astoni*, 24/I/1967. Slide and tube Nos. 3514, 3515 Canterbury Museum. Author's Catalogue number - KD 816.

Localities and collectors:

Snares Island; coll. R.A.Falla, Dec.1947, ex leafmould, taken with *Talorchestia patersoni*. Snares Island, Tunnel Point; coll. G.A.Knox, 7/I/1967, in Bullers Mollymawk nest material. Snares Island, opposite Mollymawk Islet; coll.P.M.Johns, 24/I/1967.

Diagnosis:

A small to medium-sized weakly sexually dimorphic landhopper, of the genus *Kanikania*, with large eyes, long and slender antennae 2, normal body shape, body pigmentation pattern (in spirit) of the striped type, gnathopod 1 well developed and strongly subchelate, gnathopod 2 feebly developed, weakly chelate and mitten-shaped in both sexes, peraeopods stout, pleopods somewhat reduced but all still present with 4 coupling spines, uropod 1 outer and inner ramus spined.

Chilton's holotype slide material:
Length not given, but probably about 12 mm (obtained by back-calculation from the regression of the number of podomeres on the second antenna against body length for the specimens of this species in my possession). Antenna 1: length 3 mm; flagellum shorter than peduncle, of 7 segments. Antenna 2: length 10 mm, flagellum long with 41 segments, spined like male; peduncle segment 4, 0.6 length of segment 5; segment 3, 0.5 length segment 4. Otherwise as for male described below except for the uropod 1 outer ramus which has two spines.

The sex of Chilton's holotype.
Chilton (1909) figured and described this species from a series of slides labelled A1 to A6 deposited in the Canterbury Museum. He also deposited an entire specimen labelled 'holotype' female, but this differs from his figures in a number of important points especially in the details of the palmar spination. I have dissected the first and second gnathopods from this specimen and deposited them with the holotype. Unfortunately, the remains of the whole body of the holotype specimen used to prepare the slides is no longer in existence, but the following features make the sex of the

Table 1. A comparison of the relative body dimensions of Chilton's type `female' Kanikania improvisa (in which the sexual organs are absent) with males and females from Snares Island. The comparison shows that Chilton's type is actually a male, and the species is a `feminized' one in which the adult males resemble adult females.

	Chilton's holotype	Male described in text	Author's female	Chilton's allotype female
Gnathopod 1 palm angle	144	143	117	133
Ratio of Gn 1 propod width to propod length	0.59	0.60	0.42	0.45
Ratio of antenna 2 length to width of the propod of gnathopod 1	12.1	11.7	26.8	21.28

holotype open to considerable doubt: The dactylos of gnathopod 1 nestles in a bilobed extension of the propod posterodistal margin which is a typically male feature since all the females I have examined do not show this lobed structure. The dactylos is shorter than the palm; in the female it is as long or longer. As Table 1 shows, the relative dimensions of gnathopod 1 in Chilton's slide material is typically male, being relatively more massive than is the female, with a palm angled more acutely. His very large whole specimen is typically female although somewhat masculinised by its extreme age. It possesses functional brood plates.

Allotype female (also nominated as a holotype by Chilton): Length 11.7 mm, width 1.5 mm, depth 2.4 mm. Head deeper than long. Eye round, about 0.33 head length. Antenna 1 length 1.7 mm, extends about 0.5 length of 5th segment of antenna 2 peduncle; flagellum 6 segmented, spination like male; peduncle like male. Antenna 2: length 5 mm; flagellum of 28 podomere segments.

Gnathopod 1: proportionately smaller than in male; sideplate has smaller spines; basos, ischium, merus and carpus like male but less heavily spined; propod narrower than in male, palm less angled (117°), sinuous with prominent, scarcely produced lobe fringed by prominent setae; dactyl as long or longer than palm. Gnathopod 2 and peraeopods like male. Uropods like male except that outer ramus of uropod 1 has 2 spines.

Remarks

In view of the confusion surrounding this species and its types, it seems advisable to supplement the descriptions based on the types by descriptions of additional specimens. Unfortunately, Chilton did not designate any paratypes, and his other material is in too poor condition to be used for taxonomic purposes. So other specimens, selected to be as similar to the type material as possible, are described from the collections made by P.M.Johns.

Description of new material:

Male.

Length 13.2 mm, width 1.8 mm, depth 2.0 mm. Body not very deep. Pigmentation pattern (in spirit) with weak red-brown stripes on a yellow-white background. Head deeper than long, anterior margin of cheek with a prominent seta. Eye round, about 0.33 head length, deeply pigmented. Antenna 1: length 1.5 mm, reaching 0.5 the length of the fifth segment of antenna 2 peduncle; peduncle segment 1 shortest, stouter than other peduncle segments, 1 long seta on outer superodistal margin, 1 short seta on inner margin, 2 setae near midpoint on inferior margin; peduncle segment 2 longer than segment 1, but narrower, with a long seta on outer superodistal margin, and 3 setae equidistant on inferior margin; peduncle segment 3 longer than segment 2, with 2 longer setae superodistally, 1 shorter seta inferodistally, dorsal surface with 1 longer seta midway, ventral surface with 2 setae equidistant; flagellum shorter than peduncle, with 5 podomere segments, each of which has 2 long setae on outer distal dorsal margin, and 5 shorter setae forming a partial rosette distally on the superolateral margin; terminal podomere tufted with a brush of 5 setae. Antenna 2: length 5.2 mm; peduncle segment 3 with a prominent seta inferodistally; peduncle segment 4 with a rosette of setae distally, and 2 rows of paired setae running axially; peduncle segment 5 as long as peduncle segments 4 and 3 together, with a distal rosette of setae and 4 rows of 7 setae running axially; flagellum of 32 podomere segments, each podomere having a long seta at each of the 4 distal angles. Upper lip: normal semi-circular shape with a setose margin ventrally.

Mandibles with 5-cusped incisor, lacinia mobilis 4 toothed; 5 pilose setae in the inter-tooth area; molar 18-striate, molar medial seta prominent, heavily setose, twice as long as molar width. Lower lip: scroll-shaped, deeply cleft, with tuft of fine setae distolaterally at beginning of fine setose comb on ventral margins terminating in stronger setal row proximomedially. Maxilla 1:

inner plate slender, narrowing distally; two terminal setae heavily pilose; outer plate broad, palp on outer margin, finely setose, distal margin with 9 teeth with 1, 1, 0, 5, 5, 5, 5, 4 and 4 lateral teeth; base of inner teeth with patch of very fine setae. Maxilla 2: plates broadening distally, distal spines curved inwards, inner margins of both plates bearing very fine setae, inner plate spine row terminating proximally with a stout pilose sensory seta. Maxilliped: inner plates subrectangular, distal margin with 3 spine teeth, inner one the smallest, outer two subequal; masked by row of pilose spines (7-8); pilose spines present down cleft almost to ischium; outer plate distally rounded, with row of plumose setae set back from margin and projecting beyond it to form a comb and terminating in a patch of 2-3 longer spines medially; palp short and broad, lateral lobes of segments 1, 2 and 3 projected inwards and bearing prominent setal combs set slightly submarginally; fourth segment distinct, not masked by third; outer margins of palp segments 2, 3 and 4 bearing long pairs of setae.

Gnathopod 1: coxal plate with a rounded ventral margin bearing a row of long setae; basos broad with 4 or so smaller spines anteriorly, larger ones posteriorly; ischium slightly narrower than basos, spined posterodistally; merus with posterior lobes (which sheath the margin of the reflexed propod), bearing 1 lateral spine and 1 terminal spine; carpus has prominent posterior pellucid lobes (which are propod sheathing) with pairs of spines on each lobe and at the base of the lobes, the anterior margin has small spines midway and larger ones distally; propod broad, with margins subparallel, anterior margin nearly twice length posterior, with three groups of spines equidistant, and a prominent group distally at hinge of dactylos, posterior margin slightly curved, with prominent marginal spines and a strong spine row diagonal across surface below palm; angle of palm (to anterior margin) 143°, palm nearly straight for most of its length but indented posteriorly to receive dactyl tip, palmar surface heavily sclerotised with article-tooth grooves especially anteriorly; inner palmar spine row single with 5 spines, the posterior spine being largest; outer spine row with only 3 large spines, each spine bearing an accessory blade-like structure (scionate); dactylos as long as palm, with 1 or 2 spines laterodistally at beginning of heavy sclerotisation, and 1 or 2 on palmar surface, without prominent cuticular sculpturing.

Gnathopod 2: coxal plate ventral margin rounded and spined; gill a large, simple trilobed sac; basos width about 0.33 length, 4 single spines on anterior margin, 1 on posterior; ischium subparallel, anterior margin slightly produced to a lobe, single spine posterodistally; merus posterior margin produced into a prominent lobe which broadens distally and with its surface microsculptured and setose, 2 spines at base of lobe, anterior margin slightly convex; carpus with prominent posterior lobes which are microsculptured and spined at their base, distal margin spined laterally and anteriorly; propod margins subparallel, slightly broader distally, length 3 times width, surface microsculptured, anterior margin produced to a lobe into which the dactyl engages, posterior margin less sculptured, spined at the distal angle, a row of single spines runs axially over the lateral face of the propod, palm short, strongly convex, 0.5 propod width, flanked by a row of small spines (3-4), terminating with a spine anteriorly; dactylos short, curved towards propod lobe with its tip inserting into a palmar depression distally.

Peraeopod 1: coxal plate subsquare, posterior and ventral margins slightly convex, ventral margin spined; gill about 0.5 to 0.75 sideplate width, simple sac-like; basos anterior margin concave with 2 large spines marginally and a group of two large spines distally, posterior margin with 3 large spines marginally and 1 distally; ischium slightly lobed anteriorly, with a spine posterodistally; merus broader distally, anterior margin convex with a few stout spines, posterior margin slightly sinuous with 5 groups of stout spines; carpus width about half that of merus with 2 spines midlaterally, posterior margin convex with 5-6 pairs of long spines, distal margin spined anteriorly; propod longer than carpus, tapering distally, anterior margin with 3 spines, posterior margin with 6 pairs of long spines forming a comb-like structure used for cleaning the body, distal margins with 3 long spines anteriorly; dactylos long with a strong posterior and a weak anterior spine.

Peraeopod 2: coxal plate ventral margin convex, with about 11 spines, anterior and posterior angles more rounded than for peraeopod 1; gill larger than peraeopod 1, a simple flattened sac; basos subparallel, anterior margin slightly concave with 3 long spines marginally, posterior margin slightly convex with 3 equidistant, strong, marginal spines, distal margin spined with strong pair of spines anteriorly and a spine posteriorly; ischium short, broadening distally, slightly lobed anteriorly, spined posterodistally; merus length about 0.75 that of basos, margins subparallel, anterior margin convex with 4 equidistant stout spines, posterior margin nearly straight with 5 stout spines, distal margin produced posterodistally with 3 stout spines, 1 spine anterodistally; carpus subrectangular, with margins subparallel, anterior margin with 2 spines, posterior margin with 4 pairs of stout spines, propod slightly narrower distally, anterior margin with 3 spines, posterior margin with 7 pairs of spines; dactylos not as long as that of peraeopod 1.

Peraeopod 3: coxal plate half-rounded, ventral margin spined; gill larger than gill of peraeopod 2, with distal lobe; basos teardrop shape narrowing distally, anterior margin with 6 pairs of spines, posterior margin with about 8 long spines, distal margin angles spined; ischium smaller and broader than that of peraeopods 1 and 2, subrectangular, with pair of spines anterodistally; merus broadening anterodistally, with 3 pairs of spines anterolaterally and 1 spine on posterior margin, distal margin with 1 long and 1 shorter spine anteriorly, and a pair of long spines posterodistally; carpus narrowing distally, margins almost parallel, anterior margin with 5 long marginal pairs of triplets of spines, posterior margin with 4 long spines, distal angle spined, propod long and tapering, anterior margin with 7 spines paired with stout peg-like lateral spines, posterior with 4 long spines, dactylos long and conical.

Peraeopod 4: 1.5 times longer than peraeopod 3; gill simple, plate-like; sideplate small, rounded ventrally, basos ovoid, anterior margin with 10 strong spines, posterior margin with about 9 smaller spines, distal margin spined anteriorly, rounded posteriorly; ischium small, spined anterodistally; merus slightly broadening distally, anterior margin with 5 pairs of triplets of spines, posterior margin with 4 stout spines, anterodistal angle with 4-5 prominent spines; carpus long, margins subparallel, anterior margin with 5 triplets of stout spines, posterior margin with 5 long spines paired with very small spines, posterodistal margin with 3 very long spines; propod very long, tapering, slightly curved posteriorly, anterior margin convex with 11 pairs or triplets of spines, posterior margin with 8 pairs or triplets of spines; propod long and conical.

Peraeopod 5: gill triblobed, not plicate; basos teardrop shaped, anterior margin with 7 strong spines, posterior margin with 5 very small spines, posterodistal angle recurved; ischium rhomboidal, anterodistal angle spined, posterior margin slightly produced to a conical process; merus long, broader distally, anterior margin with 4 triplets of spines, posterior margin with 4 spines, anterodistal and posterodistal angles produced into a sclerotised lobe nd spined carpus as long but narrower than merus, slightly reflexed posteriorly, anterior margin with 5 posterior margin with 2 groups of spines, posterodistal margin with a group of prominent spines; propod long, slightly narrowing distally, anterior margin with 6 and posterior margin with 4 pairs of spines; dactylos long, hardly curved, with 3 small rounded spines in an axial line.

Epimeral plates: First, anterior and ventral margins rounded, posterodistal angle produced slightly. Second and third, posterior margins straight with 1 or 2 minute spines on posterior margin, posterodistal angle only slightly produced posteriorly.

Pleopods: all present and short and broad; first is longest; third is very short; all have peduncle longer than rami, with 4 coupling spines on inner distal margin, inner ramus 0.66 length outer, all rami with sparse plumose setae, segmentation poorly developed, very fine setae present on margins but more particularly on third.

Uropod 1: peduncle as long as rami, with 4-5 spines on each dorsal margin; outer ramus with 2 spine sockets, terminating with 2 long and two short spines; outer ramus with 3 spines, terminating with 2 long and two short spines; a large inter-ramal spur is present about 0.25 ramus length. Uropod 2: peduncle has a spined dorsal surface; outer ramus with one spine dorsally, terminating in one long and one short spine; outer ramus with 2 spines on outer dorsal margin and 2 pairs of spines on the inner dorsal margin, 1 member of each pair being long and one short, the ramus terminates with 3 long spines, a strong inter-ramal spur is present. Uropod 3: much the shortest with a spined dorsal margin and a single ramus terminating in 2 larger and 1 small setae.

Telson: moderately cleft, length nearly twice width, 1 long spine on each lobe.

<u>Remarks</u>

Broodplates and the breeding season.

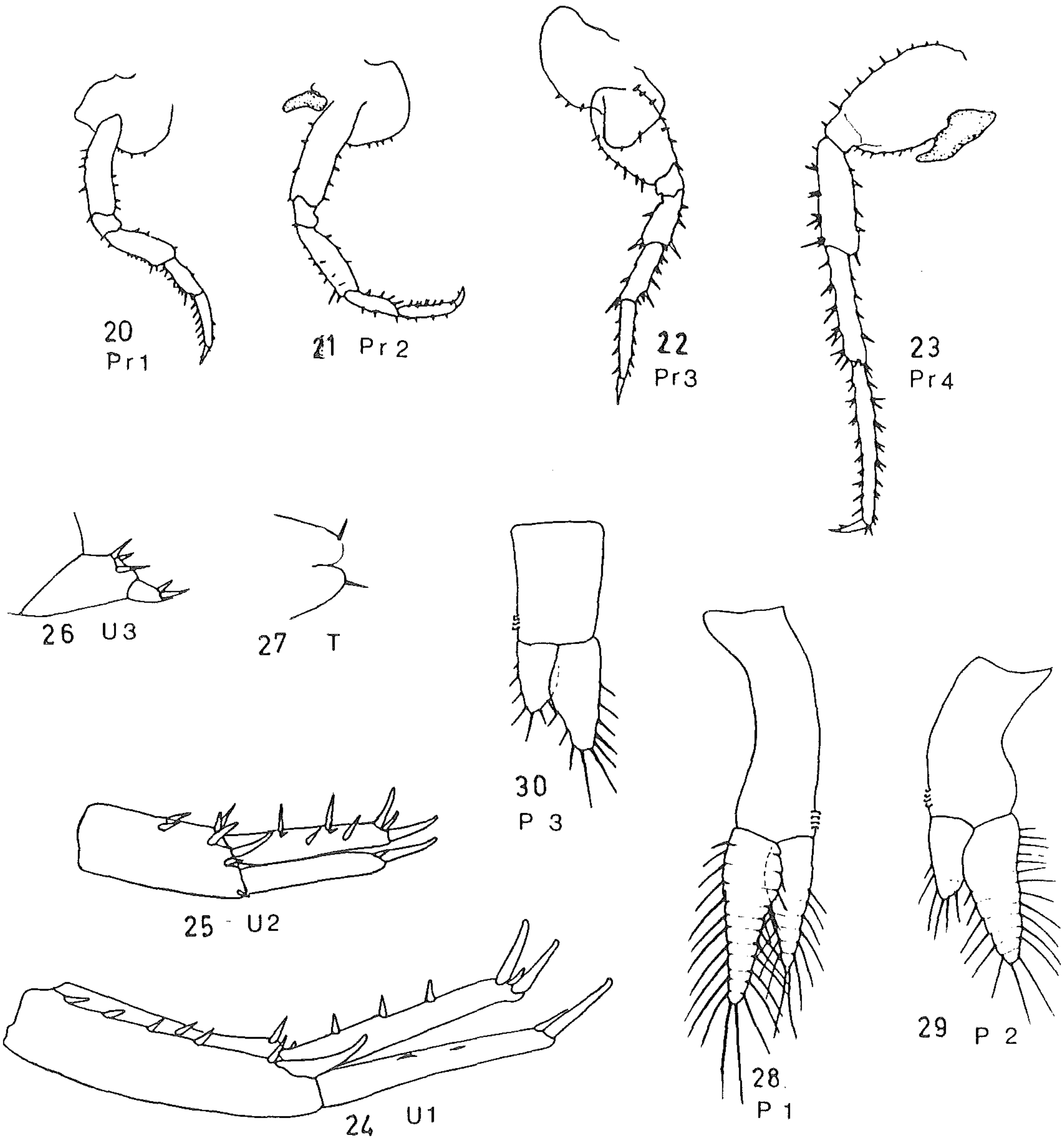
The brood plates in all females examined are in the typical winter (nonbreeding) form. In this condition they are spineless, and are much thicker, probably because they are blood filled and are functioning as accessory gills. All collections studied were made in early summer which suggests that this species has a single breeding season in late summer unlike its mainland relatives which have a prolonged breeding season over spring, summer and autumn (Duncan, 1969).

The broodplates of *Makawe hurleyi* have the same blood-filled appearance in winter, and they assist in the acclimatisation of metabolic rate to temperature in winter (Part II). Perhaps this species shows the same kind of acclimatisation. If so, it would be a major adaptation to the cold winter temperatures experienced in the subantarctic islands.

The function of uropod spines.

The presence or absence of spines on the outer ramus of uropod 1 was considered by Stephensen (1935) to be an excellent taxonomic character, and in all the species I have examined it is species specific. Spines on the outer ramus are associated with life on a friable substrate, such as sand, and they are typical of supralittoral talitrids and those living in coastal fringe forest where dry, friable soil is common. The uropods can be spread as a broad fan to spread the load when jumping and can also be used for shovelling and digging. The rami are held apart and the spines help increase the effective area of the digging 'fan'. Species which live in less friable habitats such as forest soil, hold their rami with the outer ramus under the inner, so forming a strong unit for jumping. Dorsal spines on the outer ramus tend to hinder this and so terrestrial species, as exemplified by *Parorchestia tenuis*, tend to develop naked outer rami. Many individual specimens of *K.improvisa* have all their outer ramal spines knocked off, showing that this species, too, must be holding its rami to function as a single unit for jumping rather than digging. The damaged spines could become infected so the naked condition of the *Parorchestia* species is advantageous.

The discovery of ectoparasites on the soft integumental depressions around the base of the uropod dorsal spines (Figure 62) may also provide an explanation for the phylogenetic reduction of the dorsal spination armature in terrestrial amphipods. In the parasitised landhoppers examined, over 90% of these depressions were occupied by ectoparasites. There was usually only a single ectoparasite present at each spine base, but some sites on heavily infested individuals were occupied by up to four parasites. The depression sites probably offer protection from the host's cleaning activities because they are so close to the base of the spine and are depressed below the general uropod surface. Presumably, the parasite feeds on haemolymph so the sites occupied offer a further advantage in having a thin, easily penetrated cuticle. If dorsal spines on the uropods perform no valuable function in terrestrial species, then the risk of infestation by ectoparasites offers an additional explanation for reduction in uropod spination. amphipods. The terminal spines on the uropods, on the other hand, are not reduced because they are important in jumping and in assisting the removal of exuviae during moulting.



FIGURES 20-30. Kanikania improvisa. 20, peraeopod 1. 21, peraeopod 2. 22, peraeopod 3. 23, peraeopod 4. 24, uropod 1. 25, uropod 2. 26, uropod 3. 27, telson. 28, pleopod 1. 29, pleopod 2. 30, pleopod 3.

Table 2. Analysis of covariance of the linear regression of podomere segments on the flagellum of antenna 2 (N) against body length (B) for 25 specimens from Stewart Island and 26 specimens from Snares Island belonging to Kanikania.

Sample	Mean B	Mean N (mm)	Equation of principal axis
Stewart Is.	7.57	23.24	B=1.975 + 0.240N
Snares Is.	10.88	29.08	B=-6.486 + 0.507N

ANCOVA Table

Source of variation	d.f.	S.S.	M.S.
Deviations from regression			
Within			
Stewart Is.	23	281.435	12.236
Snares Is.	24	198.095	8.254
Sum	47	479.530	10.203
Pooled	48	885.282	18.443
Differences between slopes			
Between	1	405.752	405.752
Combined	49	888.429	17.769
Between adjusted means	1	3.148	3.148

Variance ratios (ie, values of the F statistic):
Heterogeneity of variances = 1.482 for 23 and 24 d.f. - not significant at 5%.
Differences between slopes = 39.769 for 1 and 47 d.f. - significant at 0.1%.
Differences between constants = 0.171 for 1 and 48 d.f. - not significant at 1%.

Distribution.

Chilton remarked that this species was present on Stewart Island as well as Snares Island. This distribution was also given by Stephensen (1935) although he stated that his specimens did not have spines on the outer ramus of uropod 1. Hurley (1957) described a small 'female' as a hypotype and gave the localities as Snares and Stewart Islands. I have not been able to examine this specimen as it was not deposited in the National Museum and cannot be located. However, all the specimens of this species I have examined from Stewart Island show a number of distinctive differences from the Snares Island form including: no spines on the outer ramus of uropod 1, a less well developed male gnathopod 1 propod and dactylos, a palm without the terminal lobes, and generally weaker spination. To test these differences further, morphometric analyses were undertaken using analysis of covariance (Snedecor and Cochran, 1967) on the linear regression of flagellum segments on the second antenna against body length. The results given in Table 2 and illustrated in Figure 31 show that the Snares Island specimens are statistically significantly different (at 1%) from the Stewart Island specimens. The results of the morphometric analyses of other body parts given in Table 3 tend to confirm that the two populations are different.

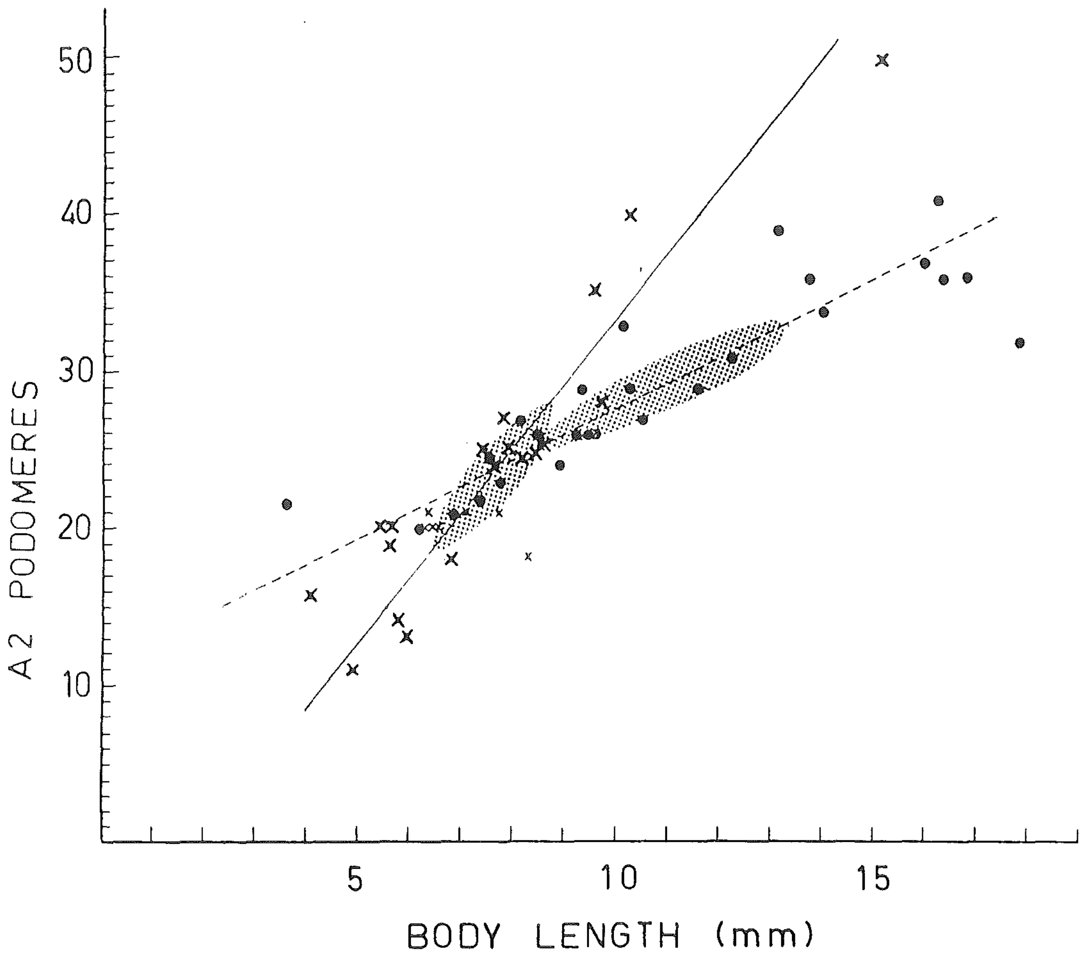

A2 PODOMERES
50
40
30
20
10
5
10
15
BODY LENGTH (mm)

Table 3. Further morphometric analyses using ANCOVA of the Stewart Island and Snares Island specimens of _Kanikania_.

	Hetero-geneity (F)	Difference between slopes (F)	Difference between intercepts (F)	Number in sample (Stewart Is., Snares Is.)
Length of antenna 2 vs podomeres on antenna 2	2.172**	9.141**	1.608ns	26,27
Length of antenna 2 vs body length	9.980**	3.632ns	7.895	25,27
Length of body vs length of outer ramus of uropod 1	63.830**	0.112ns	7.225**	25,26

ns = not significant at 5%
** = significant at 1%.

Discriminant analysis is the more usual technique employed for analysing morphometric data, but it is not as useful for amphipods because any one population contains a wide range of different sized individuals. The morphometric analysis of amphipods is further complicated by the fact that the differentiation of a body part, for example, the number of spines on the uropod 1 peduncle, depends on the age of the individual (Table 4). Since the age composition of the population, and hence the average size and degree of differentiation of the individuals in the population, varies seasonally because breeding and recruitment are seasonal, the morphometric attributes of a population are not constant. Analyses

Table 4. Morphometrics of 26 specimens of Kanikania from Snares Island and 25 from Stewart Island. The lengths are in mm. LA2 = length of antenna 2, LB = length of body, LOR1 = length of uropod 1 outer ramus, A2PN = number of podomeres on antenna 2 flagellum, NS = number of spines on uropod 1 outer ramus.

Locality	LA2	LB	LOR1	A2PN	NS
Snares Is.	7.06	16.94	1.06	36	2
	6.82	18.00	1.18	32	1
	5.65	12.35	0.88	31	1
	7.06	16.47	1.12	36	2
	7.06	13.88	1.00	36	0
	5.53	14.12	0.94	34	1
	3.41	7.53	0.59	24	1
	4.35	9.29	0.59	26	1
	5.41	11.65	1.12	29	1
	4.00	6.94	0.53	21	2
	4.24	8.94	0.65	24	0
	3.65	7.41	0.59	22	0
	4.71	8.47	0.59	26	0
	4.12	9.53	0.71	26	1
	2.71	6.24	0.53	20	0
	4.82	9.41	0.71	29	1
	6.82	3.65	0.56	22	2
	10.04	16.39	1.71	41	3
	8.27	13.25	2.39	39	2
	5.12	9.56	1.64	26	1
	3.42	7.79	1.09	23	0
	5.12	10.59	1.79	27	1
	5.81	10.18	2.05	33	2
	4.99	8.06	1.71	27	1
	7.18	16.12	1.3	37	2
Stewart Is.	2.6	6.01	0.48	13	0
	4.51	7.79	0.55	24	0
	6.83	9.7	0.77	35	0
	7.92	10.31	0.81	40	0
	2.80	5.87	0.47	14	0
	3.55	8.33	0.68	18	0
	11.07	15.3	1.13	51	0
	2.53	6.69	0.42	18	0
	4.03	8.2	0.65	24	0
	4.92	8.61	0.65	25	0
	4.10	7.45	0.61	25	0
	3.76	8.67	0.61	25	0

(continued over page)

Table 4 continued.

LA2	LB	LOR1	A2PN	NS
3.01	6.49	0.48	20	0
1.78	4.99	0.39	11	0
5.40	9.77	0.74	28	0
3.89	6.42	0.48	21	0
3.55	7.99	0.45	21	0
3.01	5.67	0.42	19	0
3.69	7.17	0.55	21	0
3.62	5.67	0.52	20	0
4.51	7.92	0.55	25	0
2.73	4.17	0.45	16	0
2.94	5.67	0.52	20	0
4.99	7.86	0.68	27	0
3.01	6.56	0.48	20	0

employing analysis of covariance techniques are not affected by these seasonal demographic changes since the analyses are directed to comparing the fundamental morphometric growth equations, the measured values are only used to establish these equations. Although measured values may vary with season or bias, growth equations are far less likely to vary significantly. Disciminant analysis discriminates between sets of measured values, so its usefulness is considerably lowered because these values are not reliable indicators, in themselves, of set (group) membership.

Nevertheless, a discriminant analysis of the data in Table 4 did separate the Snares Island and the Stewart Island specimens reasonably well. The analysis was performed on a Prime 750 computer using the SPSS discriminant analysis subprogram (Nie et al, 1975). Both direct and stepwise analyses were used, the latter using both Rao's V and the minresid criteria to determine the order of selection of the independent variables. Both stepwise criteria gave identical results which were marginally better than the direct method. Table 5 gives the results of the stepwise discriminant analysis using Rao's criterion. The variable A2PN (number of podomere segments on antenna 2) was rejected by the analysis. The discriminant function using the remaining variables discriminated successfully between the groups as can be seen by the highly significant Wilk's lambda value. However, there is a fair percentage error when this analysis is extended to classifying actual specimens since 36% of the known Snares Island individuals and 4% of the known Stewart Island individuals were misclassified into the other group when classified by their discriminant scores as calculated for each specimen by

Score = 0.74981 [standardised LA2] - 0.54767 [standardised LB] + 0.82363 [standardised LOR1],

where LA2 is length of antenna 2, LB is body length, and LOR1 is length of the outer ramus of uropod 1.

This error shows that discriminant analysis is not as suited for amphipod morphometrics analysis as is the analysis of covariance. However, both analytical methods do show that a real morphometric difference exists between the Snares Island and Stewart Island specimens of _Kanikania improvisa_, and because these two groups also differ in other morphological features, such as the presence or absence of spines on the outer ramus of uropod 1, I consider that they are two different but closely related species. The Stewart Island form, which I propose to call _Kanikania_ *motuensis*, is described below. It shows some interesting adaptations to the terrestrial state beyond those of the more primitive form, *Kanikania improvisa*, in that its antenna 2 are more slender, its gnathopods are less well developed, and its uropod 1 outer ramus is naked. The average size of individuals in the population is also smaller (4.19 mm vs 5.49 mm).

Table 5. Stepwise discriminant function analysis of the data in Table 4, using Rao's V criterion to determine the order of selection for the independent variables. The variables are coded as follows: LB = body length in mm., LA2 = length of antenna 2, LOR1 = length of the outer ramus of uropod 1 in mm, A2PN = number of podomeres on the flagellum of antenna 2. Grouping is by locality (i.e., Snares or Stewart Is.).

Wilk's lambda and univariate F-ratio with 1 and 48 degrees of freedom

Variable	Wilk's lambda	F	Probability
LB	0.885	6.218	0.161
LA2	0.772	14.171	0.0005
LOR1	0.701	20.452	<0.0001
A2PN	0.861	7.738	0.0077

Canonical discriminant functions:

Eigenvalue	0.559	Canonical correlation	0.5989
Wilk's lambda	0.641	chi-squared	20.661
d.f.	3	significance	0.0001

Standardized canonical discriminant function coefficients:

LA2	0.750
LB	-0.54848
LOR1	0.82424

Classification results:

Actual group	No. of cases	Predicted group membership: Snares Is.	Stewart Is.
Snares Is.	25	16 (16.0%)	9 (36.0%)
Stewart Is.	25 (4.0%)	1 (96.0%)	24

Percent of grouped cases correctly classified, 80.0%.

Kanikania motuensis new species

Figures 32 to 61, Figure 63.

Parorchestia improvisa Chilton, 1909:641; Shoemaker, 1935:13; Stephensen, 1935:1-20, 1938:251-252.

Orchestia improvisa Hurley, 1957:183-185.

Types:

Holotype male and allotype female: Murderers Cove, Big South Cape Island off Stewart Island, coll. R.K.Dell and B.A.Holloway, 24/I/1955, slide no. 3516, 3517, Canterbury Museum, plus tubes which contain remains of dissected specimens. Author's catalogue number - KD 780.

Localities and collectors:

Stewart Island, coll. Th.Mortensen 1 F, 21/XI/1914. S.E.Stewart Island, Small Craft Retreat, coll. R.K.Dell and B.A.Holloway, 23/I/1955 ex leafmould, M and F, taken with *Parorchestia tenuis*. S.W.Stewart Island, Lords River, R.K.Dell and B.A.Holloway, 29/I/1955, Northern Entrance, ex *Senecio* scrub. S.W.Stewart Island, Hidden Island, coll. R.K.Dell and B.A.Holloway, 28/I/1955, ex leafmould. S.E.Stewart Island, Nelly Island, coll. R.K. Dell and B.A. Holloway, 22/I/1955, ex *Senecio* and tussock leafmould, taken with *Talorchestia patersoni*. S.E.Stewart Island, Lords River, coll. R.K.Dell and B.A.Holloway, 29/I/1955, ex *Senecio* leafmould, taken with *T.patersoni*. S.W.Stewart Island, Mokinui Island, coll. R.K.Dell and B.A.Holloway, 28/I/1955, ex leafmould, taken with *P.tenuis* and *T.patersoni*. S.E.Stewart Island, Port Pegasus, coll.

R.K.Dell and B.A.Holloway, 22/I/1955, ex leafmould. Stewart Island, Kapipi, Paterson Inlet, 18/IV/1980, coll. P.Johns. S.E.Stewart Island, Kundy Island, coll. R.K.Dell, 21/V/1956, taken with T.patersoni and P.tenuis. S.W.Stewart Island, Solomans Island, coll. R.K.Dell and B.A.Holloway, 25/I/1955, ex leafmould. Stewart Island, Thule, Paterson Inlet, coll. R.K.Dell, 31/X/1948, taken with P.tenuis. Stewart Island, Port Pegasus, near wharf, coll. R.K.Dell, 25/V/1956, taken with P.tenuis. S.W.Stewart Island, Big South Cape Island, Murderers Cove, coll. R.K.Dell and B.A.Holloway, 24/I/1955, ex leafmould, taken with T.patersoni. Tommy Island Bravo Group, coll. L.C.Cadenhead and N.A.Deans, 30/XI/1981, under log in Senecio verge. Codfish Island, Mirkwood Petrel colony, coll. N.A.Deans and L.C.Cadenhead, 11/I/1982, taken with T.patersoni and P.tenuis. Codfish Island, Mephistopheles, coll. N.A.Deans and L.C.Cadenhead, 11/I/1982, tree fern pit traps, taken with T.patersoni and P.tenuis. Codfish Island, East Hut, coll. N.A.Deans and L.C.Cadenhead, Jan.1982, pit trap 100 in pakahi scrub, taken with P.tenuis.

Etymology: the name is derived from the Maori motu meaning an island.

Diagnosis:

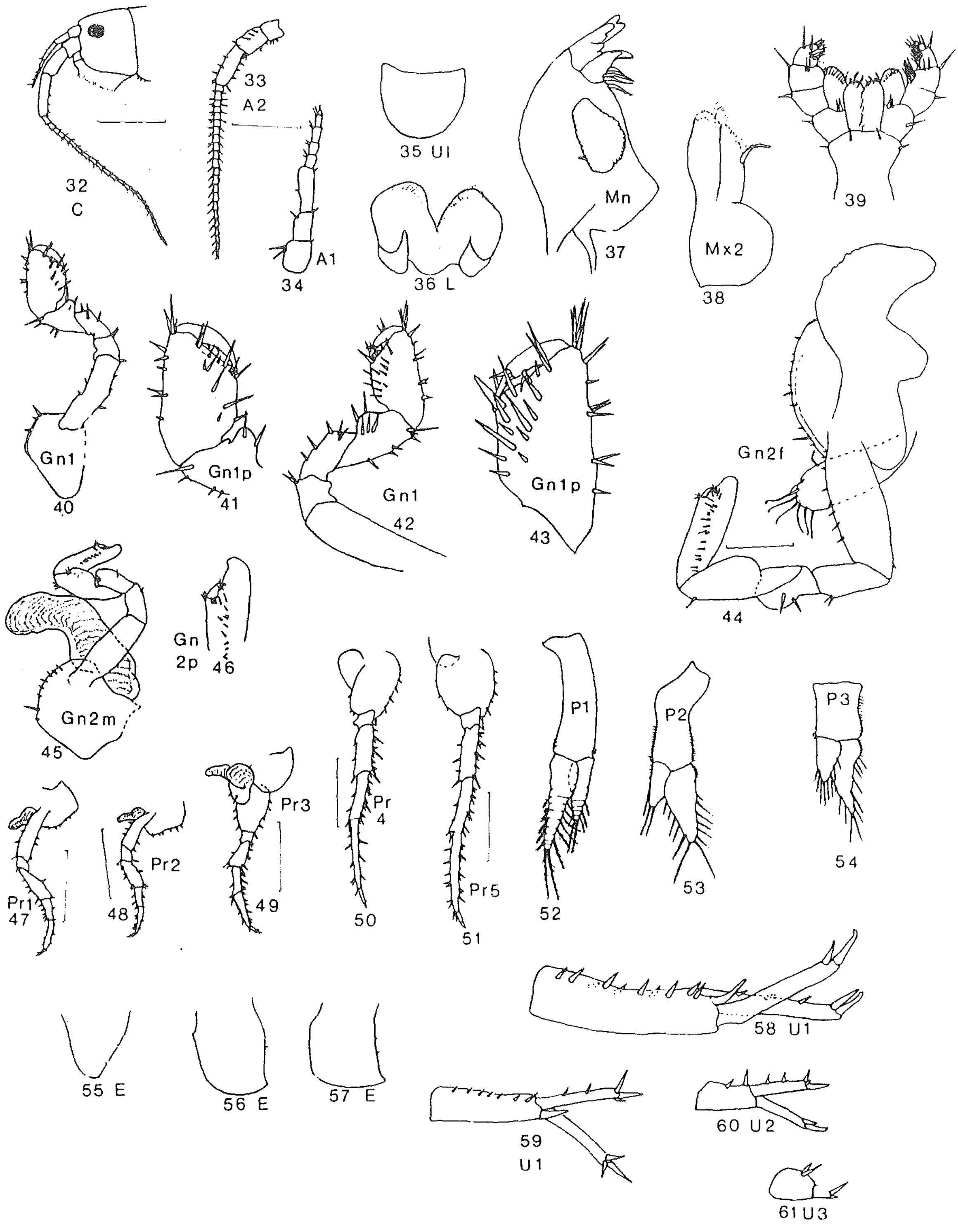
A small, weakly sexually dimorphic landhopper, of the genus Kanikania, with large eyes, long and slender antennae 2, gnathopod 1 well developed and strongly subchelate, gnathopod 2 feebly developed, weakly chelate and mitten shaped in both sexes, peraeopods stout, pleopods somewhat reduced but all still present with only 2 coupling spines, uropod 1 outer ramus naked.

Description:

Male:

Length 8 mm, width 1.2 mm, depth 1.9 mm. Body not very deep. Pigmentation pattern with red-brown stripes on yellow-white background. Head deeper than long. Eye round, about 0.33 head length, deeply pigmented. Antenna 1: length 0.7 mm, extends about 0.33 the length of the fifth segment of antenna 2 peduncle; peduncle segment 1 the shortest, 2 large spines on superodistal margin, otherwise naked; peduncle segment 2 longer than 1, spined on infero- and superodistal margins, otherwise naked; peduncle segment 3 longer than segment 2, spined inferodistally, dorsal surface with 1 spine midway; flagellum shorter than peduncle, 5 segmented, spined dorsodistally. Antenna 2: length 4.1 mm; peduncle segment 3 with 3 spine rows of about 4 spines running axially; peduncle segment 4 twice length of segment 3, with rosette of setae distally and 3 rows of paired setae running axially; peduncle segment 5 as long again as segment 4, with 4 rows of spines running axially, and with between 4 and 7 spines per row; flagellum of 24 podomere segments, with a terminal tuft of about 5 setae tightly bound; each podomere segment has 3 pairs of long spines at the distal margin corners that the inner superodistal margin has 3 spines in a group.

Upper lip: normal semi-circular setose ventral margin. Mandibles: with 5-cusped incisor, lacinia mobilis 4-5 toothed,



FIGUREs 32-61. Kanikania motuensis new species. 32, cephalon. 33, antenna 2. 34, antenna 1. 35, uppper lip. 36, lower lip. 37, mandible. 38, maxilla 2. 39, maxilliped. 40, gnathopod 1 male. 41, gnathopod 1 male propod. 42, gnathopod 1 female. 43, gnathopod 1 female propod. 44, gnathopod 2 male. 45, gnathopod 2 female. 46, gnathopod 2 male propod. 47, peraeopod 1. 48, peraeopod 2. 49, peraeopod 3. 50, peraeopod 4. 51, peraeopod 5. 52, pleopod 1. 52, pleopod 2. 53, pleopod 3. 55, epimeral plate 1. 56, epimeral plate 2. 57, epimeral plate 3. 58, uropod 1 male. 59, uropod 1 female. 60, uropod 2 male. 61, uropod 3 male.

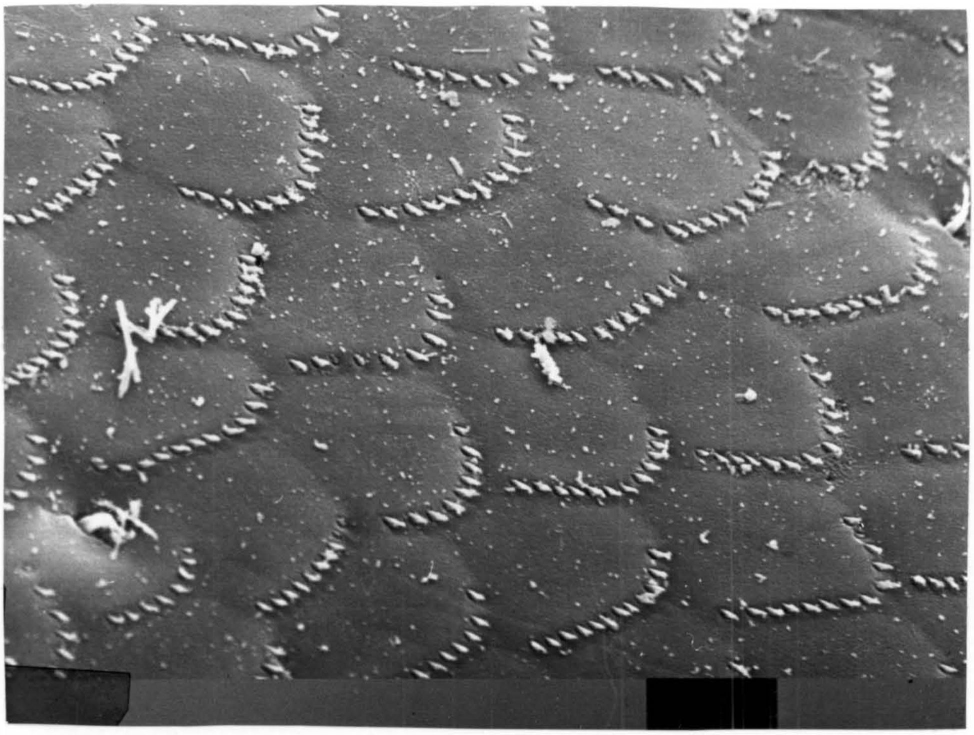


FIGURE 62. Cuticular structure of Kanikania improvisa. Single rows of mesopores are arranged in arcs near the posterior margins of the cuticular polygons. Macropores are also present. The scale bar represents 9 micrometres.

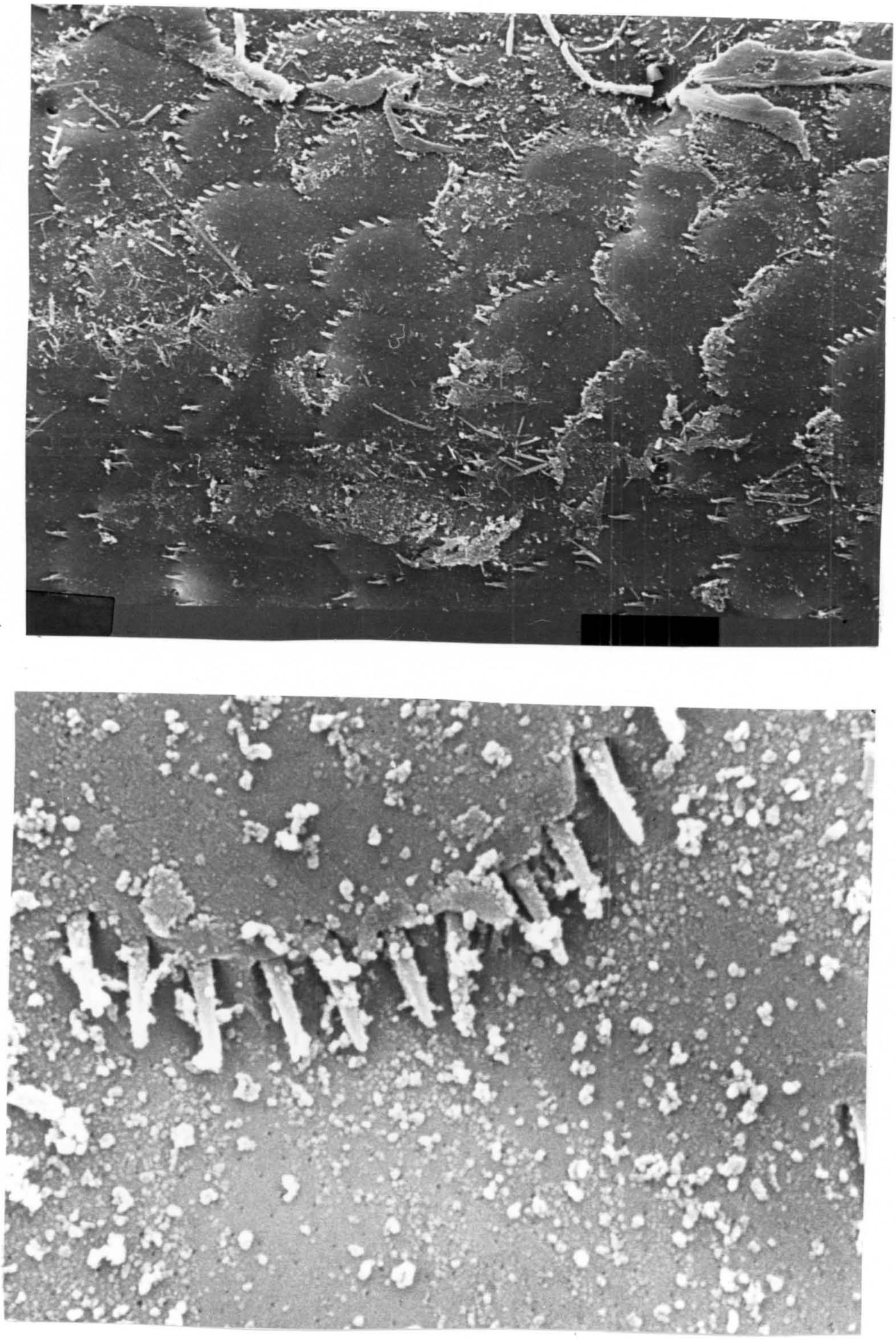


FIGURE 63. Cuticular structure of Kanikania motuensis. Note the general similarity to K.improvisa, but the projections are longer. Scale bars: upper micrograph 20 micrometres; lower 2 micrometres.

molar 20-striate, molar medial seta prominent. Lower lip: scroll-shaped, deeply cleft, with outer margins finely setose, inner heavily setose in 2 main brush-like rows. Maxilla 1: inner plate slender, narrowing distally, 2 terminal setae heavily pilose; outer plate broad, palp on outer margin, finely setose, distal margin with 9-10 strong teeth with 1, 1, 0, 4, 4, 4, 4, 4, 4 lateral teeth, base of inner teeth with a few fine setae. Maxilliped: inner plates with 3 distal teeth not masked by pilose setae set between them; outer plates rounded distally with a double row each of 9-10 setae set back from the margin and projecting beyond it to form a comb, face of the plate has a group of 4 large spines; palp broad, terminal segment not masked, bearing terminal tuft of setae; segments 3 and 2 inner margins produced and bearing a row of 6-8 setae set back from the margin but projecting beyond to form a comb; distal margins with a pair of strong spines frontally and a single strong spine on outer margin.

Gnathopod 1: coxal plate rounded ventrally, with 4 strong spines; basos long, broadening distally, anterior margin concave with 3 spines, posterior margin convex with 2 stronger spines, posterodistal angle with 1 spine; ischium slightly narrower than basos, subrectangular, anterior margin slightly excavate, 2 spines at posterodistal margin; merus posterior margin produced into a sculptured pellucid lobe, with single spines proximal, distal and lateral to it, the lateral face of the merus has a short spine row; carpus posterior margin produced into prominent sculptured pellucid lobe which sheathes the reflexed propod, the lobe has two large spines on each side, posterior distal angle spined, anterior margin angled convexly with two marginal spines midway and two large spines at anterodistal angle; propod margins parallel, anterior margin with 4 spines set back from the margin on each face equally spaced, the shorter posterior margin has 2 strong spine pairs; lateral face of propod has 2 irregular rows of about 6 spines angled below palm posteriorly, medial face has 2 rows of stronger spines; palm sinuous, excavate proximately, produced mesodistally, and strongly convex distally, sclerotised and ridged, flanked by a single row of 5 spines, terminating in a pair of strong spines; dactylos as long or longer than palm, with a strong inner spine towards the base.

Gnathopod 2: coxal plate convex, strongly spined; gill trilobed, scarcely plicate; basos widening medially, narrower proximately and distally, with 3 small marginal spines on anterior margin, 1 on posterior; ischium spined at posterodistal angle, anterior margin slightly produced; merus posterior margin produced into a sculptured pellucid lobe, with one spine near posterodistal angle; carpus anterior margin naked, convex but nearly straight, posterior margin produced into a lobe, with a group of 3 spines at posterodistal angle and a pair at anterior distal angle; propod mitten-shaped, long with margins subparallel and naked, an irregular row of 7-9 spines run axially over both inner and outer faces to the base of the palm, posterior margin is produced into a long scabrous (sculptured) pellucid lobe, palm short, strongly convex so that the dactyl appears to 'bite' into the propod lobe, anterior end of palm with a pair of long spines, a row of short spines flanks palm, and a group of longer spines terminate it; dactylos short, about 0.5 propod width.

Peraeopod 1: Coxal plate ventral margin only slightly curved convexly, ventral margin with 8 or so marginal spines, the largest anteriorly; gill simple; basos long, wider distally, anterior margin somewhat concave with 2 marginal spines distally, posterior margin convex with 5 larger spines equally spaced marginally, distal angles spined; ischium subsquare, anterior margin slightly produced, posterior angle with a pair of spines; merus widening distally, anterior margin with 2 large spines, posterior with 5 (the most proximal being a pair of spines), distal angles each with a pair of strong spines; carpus subrectangular, anterior margin with a single short spine, posterior margin with 5 or so pairs of strong spines; propod slightly recurved posteriorly, anterior margin with 2 pairs, posterior margin with 4 pairs of strong spines; dactylos long, strongly spined posteriorly.

Peraeopod 2: coxal plate subsquare, ventral margin spined; gill simple; basos anterior margin very concave with 2 marginal spines, posterior margin convex with 3 marginal spines; ischium subsquare with anterior margin slightly produced, spined at posterodistal angle; merus broadening distally, anterior margin with 2 spines, posterior margin with 5 spines, anterior distal angle with a pair of spines, posterodistal angle with 3 spines; carpus shorter than propod, anterior margin straight with a single spine, posterior margin with 4 pairs of strong spines; propod anterior margin with 2 groups of spines, posterior margin with 3 groups of spines; dacylos long.

Peraeopod 3: coxal plate margins spined; gill about 0.5 basos in size, lobed; basos teardrop shaped narrowing distally, anterior margin with 6 spines, posterior margin with 5 spines some of which are bifid, distal angles spined; ischium small, subrectangular, spined anterodistally; merus broadening posterodistally, anterior margin with 3 groups of strong spines, posterior margin with a single spine, distal margins spined; carpus subparallel, anterior margin with 3 groups of strong spines, posterior margin with a single spine, distal angles spined; propod long, tapering distally, anterior margin with 4 pairs of strong spines, posterior margin with 2 pairs of spines.

Peraeopod 4: coxal plate rounded, nearly naked; gill trilobed; basos ovate, with about 7 spines on anterior margin, posterior margin with 7 spines, posterior distal angle rounded and somewhat produced; ischium posterior margin angular, spined on anterodistal angle; merus broadening distally, anterior margin with 4 pairs of strong spines, posterior margin with 2 pairs of spines, distal margins spined; carpus subparallel, slightly recurved posteriorly, anterior margin with 4 triplets of strong spines, posterior margin with 2 pairs of spines; propod long, subparallel, anterior margin with 5 spines, posterior margin with 4 triplets of strong spines; dactylos long and tapering.

Peraeopod 5: coxal plate small, semicircular, almost naked; basos pyriform shape, anterior margin with 6 spines, posterior margin produced with 5 very small spines; ischium rhomboidal, anterodistal angle spined; merus anterior margin with 4 groups of strong spines, posterior margin with 4 spines, distal angles spined; carpus anterior margin with 4 groups of strong spines, posterior margin with 2 pairs of small spines; propod long, only slightly tapering, anterior margin with 6 groups of spines, posterior margin with 5 groups of spines, dactylos long, scarcely curved.

Epimeral plates: first, anterior and ventral margins rounded, posterodistal angle only slightly produced; second and third, subsquare, with posterodistal angle slightly produced, posterior margin with 2 very small spines.

Pleopods all present, first the longest, third the shortest,

all are short and broad; segmentation rudimentary; inner rami on each shorter than outer; a pair of coupling spines (retinaculae) present on all; outer margins of peduncle with fine pilose setae, inner margins with very fine setae.

Uropod 1: peduncle with a row of 6 spines on outer (lateral) dorsal margin and 7 spines on inner (medial) dorsal margin; a large inter-ramal spur is present; outer ramus without marginal spines, terminal spination with 2 large (1 of these scionate) and 2 smaller spines; inner ramus with 2 marginal spines, 2 large and 2 small terminal spines (2 of which are scionate). Uropod 2: peduncle with axial rows of 2 and 4 spines dorsally, an inter-ramal spine is present, outer ramus naked, inner with 2 spines. Uropod 3: peduncle with 2 spines telson with a single long spine on each lobe.

Female:

Length 12.7 mm, width 2.2 mm, depth 2.5 mm. Antenna 1: length 1.8 mm, with 7 podomere segments, peduncle segment 3 with 1 spine dorsally, 2 small spines ventrally. Antenna 2: length 6.6 mm, flagellum of 30 podomere segments.

Gnathopod 1: basos anterior margin nearly straight, with 6 spines, posterior margin convex with 2 spines, posterodistal angle with 1 long and 4 very small spines; ischium with 4 spines at posterodistal angle; merus with posterior margin produced; carpus posterior margin produced into prominent lobes with 3 strong spines at base of lobe and 2 on margin, anterior margin convex with 2 spine groups, one with 1 and the other with 3 spines, anterior distal angle with 4 spines; propod margins subparallel, anterior margin with 5 groups of spines, posterior margin with 4 spines, 2 rows of strong spines run more or less axially on the medial face with 4 spines per row, palmar angle 123°, palm sinuous, flanked by a single row of 5 small spines, posterodistal angle with 4 stronger spines; dactylos longer than palm.

Gnathopod 2: basos anterior margin with 8 spines; ischium longer than wide, merus posterior margin with pellucid lobe with 2 strong spines at its base; propod long, slightly broadening distally, mitten-shaped, palm about 0.33 propod width.

Peraeopod 1: basos anterior margin with 6 spines, posterior with 3 spines; merus anterior margin naked; propod anterior margin with 3 pairs, posterior margin with 5 pairs of spines.

Peraeopod 2: oostegite as long as basos; basos has 3 spines on each margin; propod anterior margin with 3 groups of spines, posterior margin with 5 groups of spines.

Peraeopod 3: basos anterior margin with 7 groups of spines all of which are scionate, posterior margin with 7-8 longer spines; carpus anterior margin with 5 groups of strong spines, posterior margin with 2 spines; propod anterior margin with 5 groups of spines, posterior margin with 3 groups of spines.

Peraeopod 4: basos ovate with 8 spines on anterior margin and 9 on posterior; merus anterior margin with 4 groups of spines, posterior margin with 3 spines, carpus posterior margin with 2 spines; propod anterior margin with 7 groups of spines, posterior margin with 5 spines.

Peraeopod 5: basos anterior margin with 7 spines, posterior margin rounded and somewhat scalloped, with about 9 minute spines; carpus posterior margin with 3 groups of spines; propod margins with about 7 groups of spines on each.

Oostegites about as long as the basos of peraeopod 3, with about 7-11 setae, a few setae are weakly curl-tipped.

Uropod 1: peduncle spine rows of 6 and 5 scionate spines, inner ramus with 3 marginal spines. Uropod 2: inner ramus with 3 marginal spine pairs.

Remarks

This species inhabits off-shore islands and exposed coastal sites such as peninsulas. It is typical of the genus in living only in high conductivity soils. Friend (1980) has described *Tasmanorchestia annulata* which occurs in the same kind of habitat in Tasmania. Of some possible significance is the fact that this Australian species, too, is strongly striped.

The greater degree of spination shown by the female allotype is because it is an older animal than the male.

Kanikania rubroannulata (Hurley, 1957)

Figure 64

Orchestia rubroannulata Hurley, 1957: 179-183, figs 11 & 12

Localities and collectors:

Karewa Island, Bay of Plenty, coll. R.A.Falla, 29/II/1949, ex leafmould. Stephens Island, coll. R.R.Forster, 14/V/1950. Kapiti Island, coll. J.T.Salmon, 1950. Little Barrier Island, Te Araroa, East Coast, North Island, coll. D.E.Hurley, ex leafmould. Omaio, East Coast, North Island, coll. D.E.Hurley, January, 1951. Cuvier Island, N.W.Bay, coll. K.Wise, 18/I/1972, beneath nikau, Auckland Museum P/S 782. Whitianga Rock Reserve, Coromandel Peninsula, coll. K.W.Duncan, 17/XII/1981 in pohutukawa litter. Shakespear Regional Park, Site 2, Whangaparaoa Peninsula, Auckland, North Island, coll. K.W.Duncan, 22/XII/1981, in pohutukawa litter. Mokohinau Island off North Island, New Zealand, coll. A.E.Wright, 20/V/1979, litter, mixed forest, Auckland Museum P/S 928, KD 827. N.W.Bay, Mayor Island, coll. K.A.J.Wise, 8/XII/1966, in leaf litter, Auckland Museum P/S 137, KD 829. Westend, Green Island, coll. J.A.F.Jenkins, 26/IV/1967, Auckland Museum P/S 275, KD 830 and P/S 277, KD 836. N.W.Bay, Mayor Island, coll.K.A.J.Wise, 8/XII/1966, ex litter in pohutukawa forest at top of low ridge, Auckland Museum P/S 144, KD 835. Noisies Island (Otata Island), Hauraki Gulf, North Island, New Zealand, coll. K.A.J.Wise, 10/XII/1979, leaf litter, Auckland Museum P/S 964, KD 837. Nikau Grove, south side West Ridge, Cuvier Island, coll. K.A.J.Wise, 18/I/1972, in fallen nikau palm leaf bases, Auckland Museum KD 841. West side Shoe Island (off west coast Thames County, North Island, New Zealand), in pohutukawa leaf litter, Auckland Museum P/S 273, KD 842. Main track, Tawhiti Rahi Island, Poor Knights Island group, coll. K.A.J.Wise,10/XII/1980, lower slopes, rock outcrop, leaf litter, Auckland Museum P/S 990, KD 843.

Remarks I have not had the opportunity to examine the types of this species as they have not been deposited in the National Museum and cannot be located.

Hurley (1959) suggested that the distribution of this species, as it was then known, was related to the presence of highly phosphatic soils caused by bird droppings from mainly colonial birds, and soil overturn through burrowing. However, in many places, such as the Whangaparaoa Peninsula, they live in soils which are guano poor.

This species is a member of a community of salt-tolerant coastal organisms typified by the ngaio (*Myoporum*) or pohutukawa trees. The deposition of salt in sea mist, spray and splash causes these coastal fringe soils to have a high salt load which may reach high osmotic pressures through concentration by evaporation. The ability of *K.rubroannulata* to tolerate such soils enables it also to live in guano-rich soils since these are also high conductivity soils. The species is not dependent however, on the presence of guano.

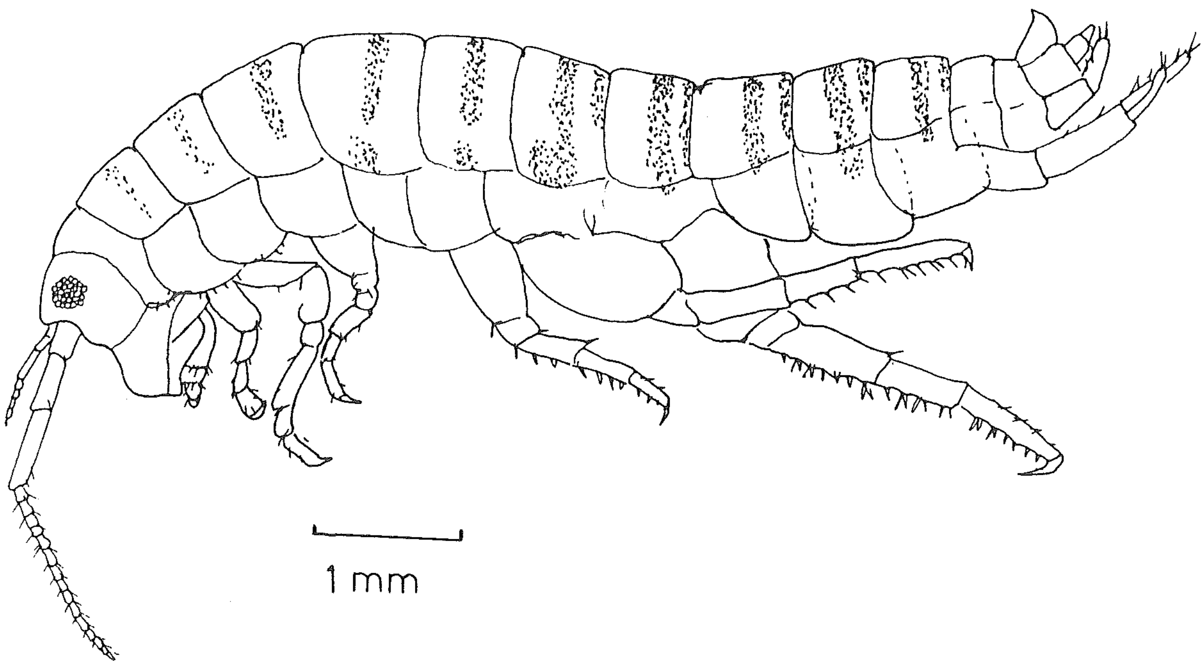


FIGURE 64. Lateral aspect of Kanikania rubroannulata showing pigmentation pattern.

Hurley further considered two mechanisms to account for the present geographical distribution of this species: transport by birds (Segerstrale, 1954; Rosine, 1960), and dimunition from a previous wider distribution to a present day relict distribution. He favoured the latter even though transport by birds is possible when amphipods are caught up in mud on the bird's feet or in feathers. Warham et al (1977) reported that numerous red-brown amphipods (Kanikania?) were observed eating feathers on chicks of the mottled petrel (Pteroderma inexpectata) on the Snares Islands. Thus it is not at all unlikely that some individuals may become caught up in the feathers of adult migrant birds.

But the distribution of K.rubroannulata is not relict as Hurley thought. The species is too abundant and widespread on both the mainland and off-shore islands for it to be relict. And since it occurs widely in a region of recent volcanism, its distribution has not been restricted by volcanic activity as he thought.

In his paper on Orchestia vaggala on the Galapagos Islands, Bowman (1977) listed other mechanisms to account for the presence of landhoppers on an island, including: (1) local origin from beachhoppers, (2) introduction on vegetation introduced by man, (3) rafting on drifting vegetation, (4) transport by birds, (5) gradual dispersal as components of the land mass subsided and others emerged in geological time. Additional mechanisms not mentioned by Bowman include a vicariance origin and dispersal on rafts of continental fragments. Land mass emergence and subsidence could help explain the distribution of the species in this genus with the most primitive in the southern (Snares) part of the New Zealand area, and the most advanced in the northern. K.improvisa was, according to this view, isolated on the Snares as the mass of the Campbell Plateau sank beneath the sea. K.improvisa probably has not evolved significantly from that time since occupies a very limited area, and so it has preserved an ancestral transitional state. K.motuensis was in turn isolated on Stewart Island some time later. This species has lost those impediments to terrestrial life, the spines on the dorsal margin of the outer ramus of uropod 1, and its antennae have become slightly shorter. The remaining member of the genus, K.rubroannulata, lives on the northern edge of the New Zealand land mass, an area characterized by its very great geomorphologial activity. Here volcanic and other activity has formed recent new islands or laid waste old areas, while marine transgressions or regressions have alternately flooded old habitats or exposed new ones (Lillie, 1980; Suggate, 1976, 1980; Brothers and Delaloye, 1982).

K.rubroannulata seems well able to persist in such a geologically active area since it is a vigorous coloniser. It has evolved further from the ancestral stock type than have the other species in the genus in having shorter antennae 2 with more delicate setae of the 'terrestrial' type, naked outer rami on uropod 1, vestigial pleopods 2 and 3, and large gills.

In Part II it is shown that the pleopods in terrestrial talitrids are used to agitate the film of water surrounding the thoracic gills and the eggs in gravid females (Duncan, 1969, 1980). Thus only the first pair of pleopods are necessary, and there is a general tendency for pleopods 2 nd 3 to become reduced or vestigial in the more advanced species. K.rubroannulata shows this in having its pleopods 2 and 3 reduced to vestigial stumps.

The respiratory area of the gills in any species seems to be inversely related to the average environmental temperature experienced by that species. Tropical talitrids have highly folded and lobed gills which provide a large respiratory area. Southern species, such as those on South Island, Snares or the Subantarctic Islands, have small sac-like gills without foldings or lobes. This is a reflection of the greater solubility of oxygen in cold water than in warm water. Therefore, for a given metabolic rate, larger gills are required by species living in warm places than those living in colder places. Gill size is therefore adaptive, and is not indicative of the evolutionary status of the species.

It may be doubted if shorter antennae are more advanced in this group, especially since the supralittoral Orchestia often have short antennae while many terrestrial species have long antennae. Possession of long antennae per se does not automatically indicate that the species is more advanced or not. Terrestrial species use their antennae for exploring their environment or manipulating females during copulation. If the terrestrial species copulates without using its antennae, then long antennae can be disadvantageous because they take more cleaning and their excuviae are more difficult to remove during moulting. This is exemplified by Talitroides topitotum living on the Whangaparaoa Peninsula immediately inland from the beach fringe forest inhabited by K.rubroannulata. Most individuals have damaged or shortened antennae, whereas K.rubroannulata, with its short antennae does not. The short antennae here have evolved parallel to the supralittoral condition, although the parallelism is superficial since they are finely setose and delicate, not stout with strong setae as in supralittoral species. The habitat occupied by K.rubroannulata is fairly friable and so is similar to that inhabited by supralittoral amphipods, hence the similarity in antenna 2 morphology.

No member of this genus has yet been found on the South Island. The marine fringe forest habitat in Canterbury and Otago is occupied by the ubiquitous Makawe hurleyi which is also a vigorous coloniser having an off-shore (Chathams Islands) and mainland distribution. It is possible that an as yet undiscovered South Island species of the Kanikania group exists, but since the pohutukawa/rata forest in which it would live has been profoundly modified or destroyed in many southern regions, its distribution will be patchy and local. The grassland dwelling M.hurleyi and Talorchestia patersoni occupy the fringe vegetation which has largely replaced this coastal forest.

Hurley mentioned that this species is easily identified in spirit by its striped pigmentation pattern. It is true that this striping is very marked, but like all amphipod pigmentation patterns it fades eventually when exposed to light and alcohol so that after prolonged storage the specimens are no longer pigmented.

Genus *Makawe* new genus

Diagnosis

Plesiomorphic landhoppers like *Transorchestia* but not as robust, with pleopod peduncles setose, all pleopods present, and a hooped body pigmentation pattern; brood plates long, delicate and narrow, and setose only distally; female gnathopod 1 without brood plates.

Etymology: Makawe is a Maori word for 'hair', an allusion to the 'hairy' appearance of the pleopods.

Type species: *Orchestia hurleyi* Duncan, 1968.

Other species: *M.insularis* (Chilton, 1909); *M.maynei* (Chilton, 1909); *M.otamatuakeke* new species; *M.parva* (Chilton, 1909); and *M.waihekensis* new species.

Remarks

The members of this group tend to be southern in their distribution, with a strong subantarctic element. They occupy coastal or strand situations and are intermediate between the supralittoral *Transorchestia* and the more terrestrial inland species.

Makawe hurleyi (Duncan, 1968)

Figures 65 to 100

Types:

Holotype male: Riccarton Bush, Christchurch, New Zealand, lodged in the Canterbury Museum. Paratypes have been lodged in the National Museum, Wellington.

Localities and collectors: Dunedin, Taieri and Tokomairiro Plains, North-eastern Otago, Canterbury Plains (numerous localities), K.W.D., 1964-1967. Riccarton Bush, J.Warham, 23/IX/1966. Woodhall Gardens, Dunedin, S.Duncan, 21/VIII/1977. Whare Flat, Dunedin District, C.L.W.(Wilton?), 4/I/1966. Wainakarua Reserve, S43 3439, K.W.D., 27/VIII/1977. Trotters Gorge, North Otago, K.W.D., 27/VIII/1977. Goodwood Scenic Reserve, K.W.D., 27/VIII/1967, in stock damaged coastal forest litter, Rakaia River road bridge, north side, K.W.D., 20/VIII/1977, in exotic grass litter under willow. Claremont Bush Reserve, West of Timaru, 44°23'S 171°06'E, in podocarp-hardwood litter. Kaituna Valley Bush, 43°44'S 172°42'E, P.M.Johns, 12/VI/1960. Kennedys Bush, Christchurch, A.J.McLeod, 7/I/1979. Sugar Loaf Bush Reserve, Christchurch, K.W.D., 30/XII/1979. Jollies Bush, Christchurch, K.W.D., 30.12.1979. Tokomairiro River bank, 1.6 km from mouth, South Otago, 46°15'S 170°00'E, C.L.W.,(Wilton?), 25/XII/1967. Peel Forest, Canterbury, 43°55'S 171°16'E, in ecotone. Eastern slopes of Mt. Peel, 923 m, 18/VI/1967, under *Celmesia* and flax. Kelseys Bush, Waimate, P.M.Johns, 15/IV/1968, in *Fuchsia*-ngaio litter. Cass Field Station, Canterbury, P.M.J., 3/IX/1967, under logs in beech forest behind

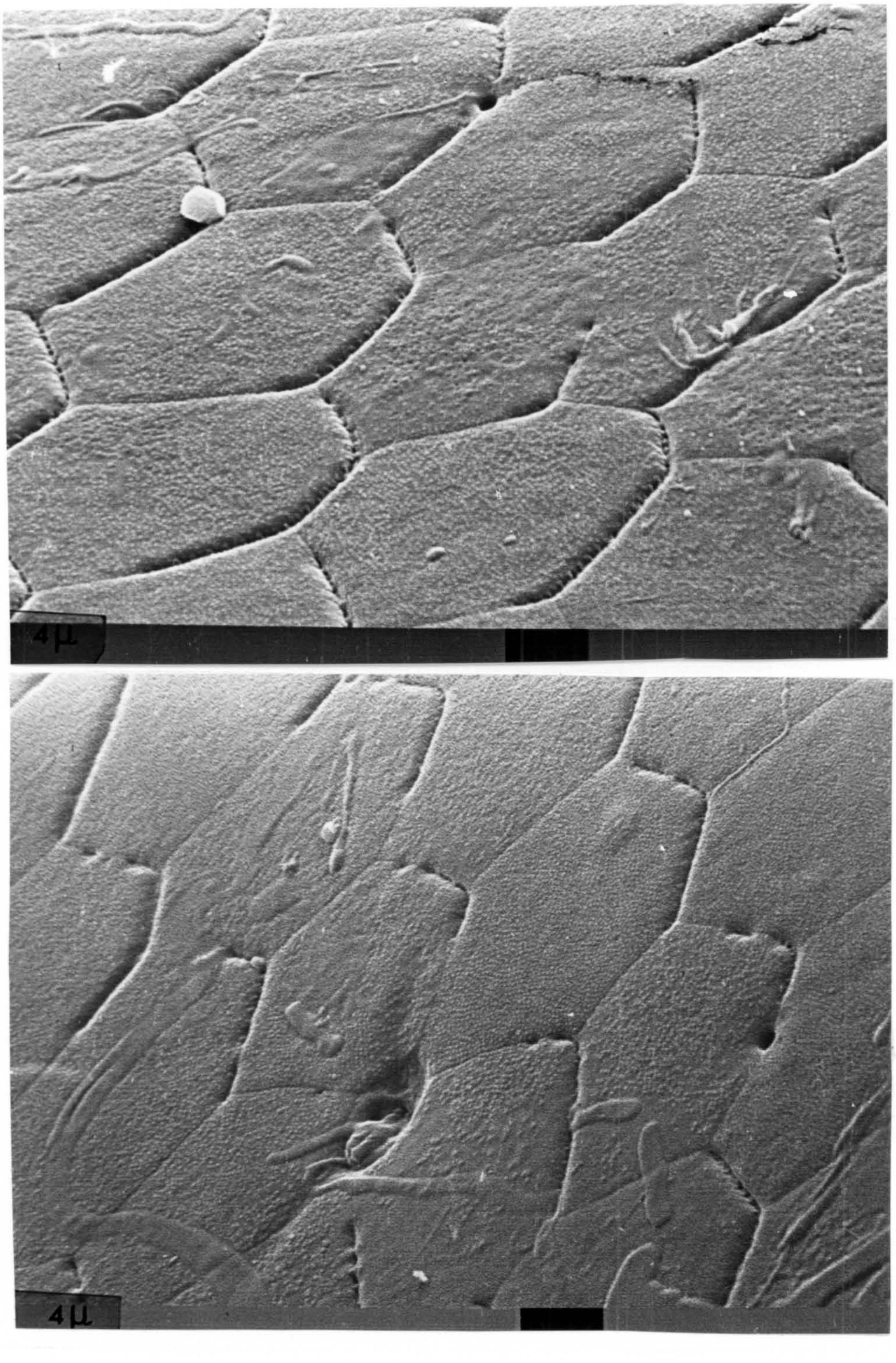
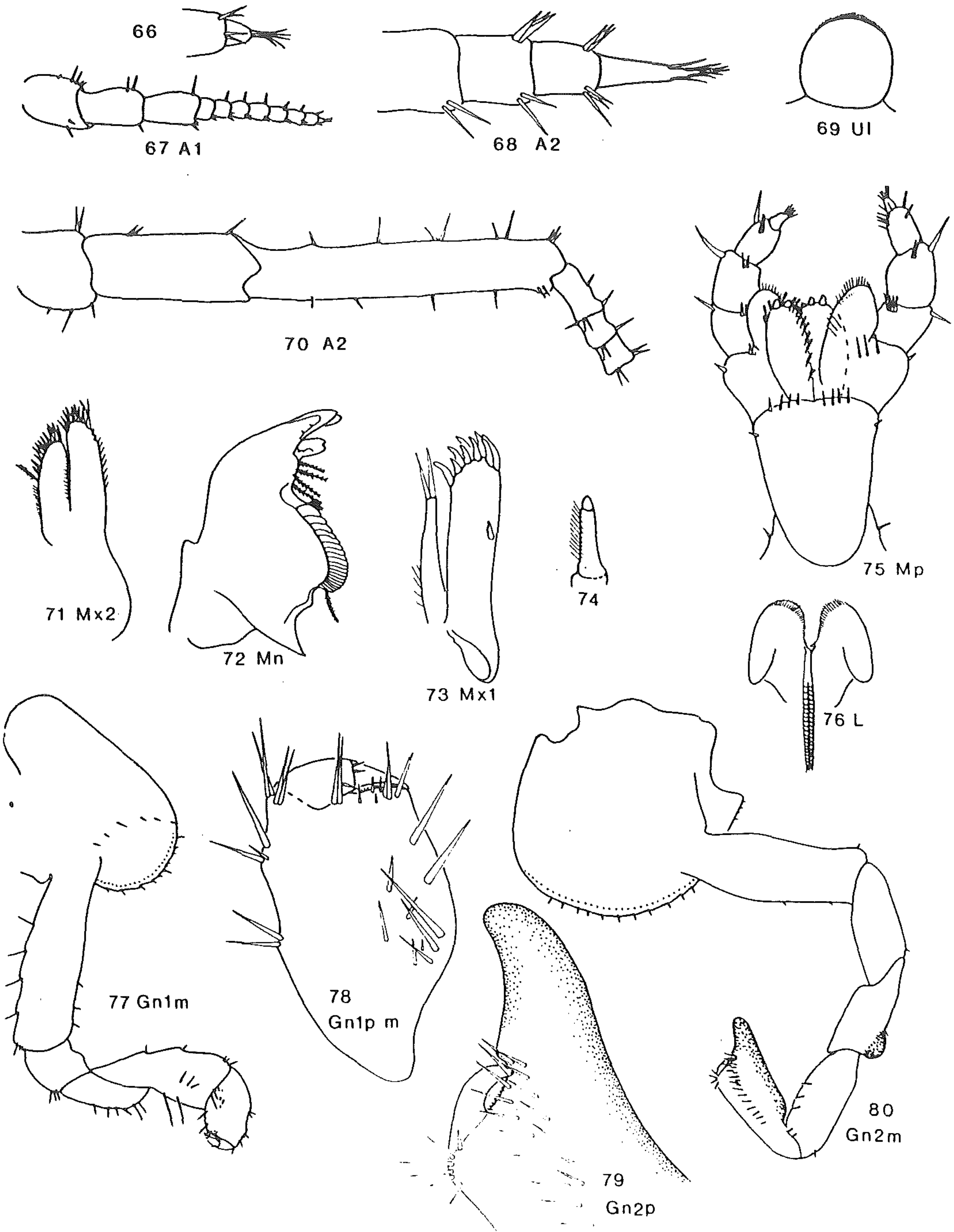
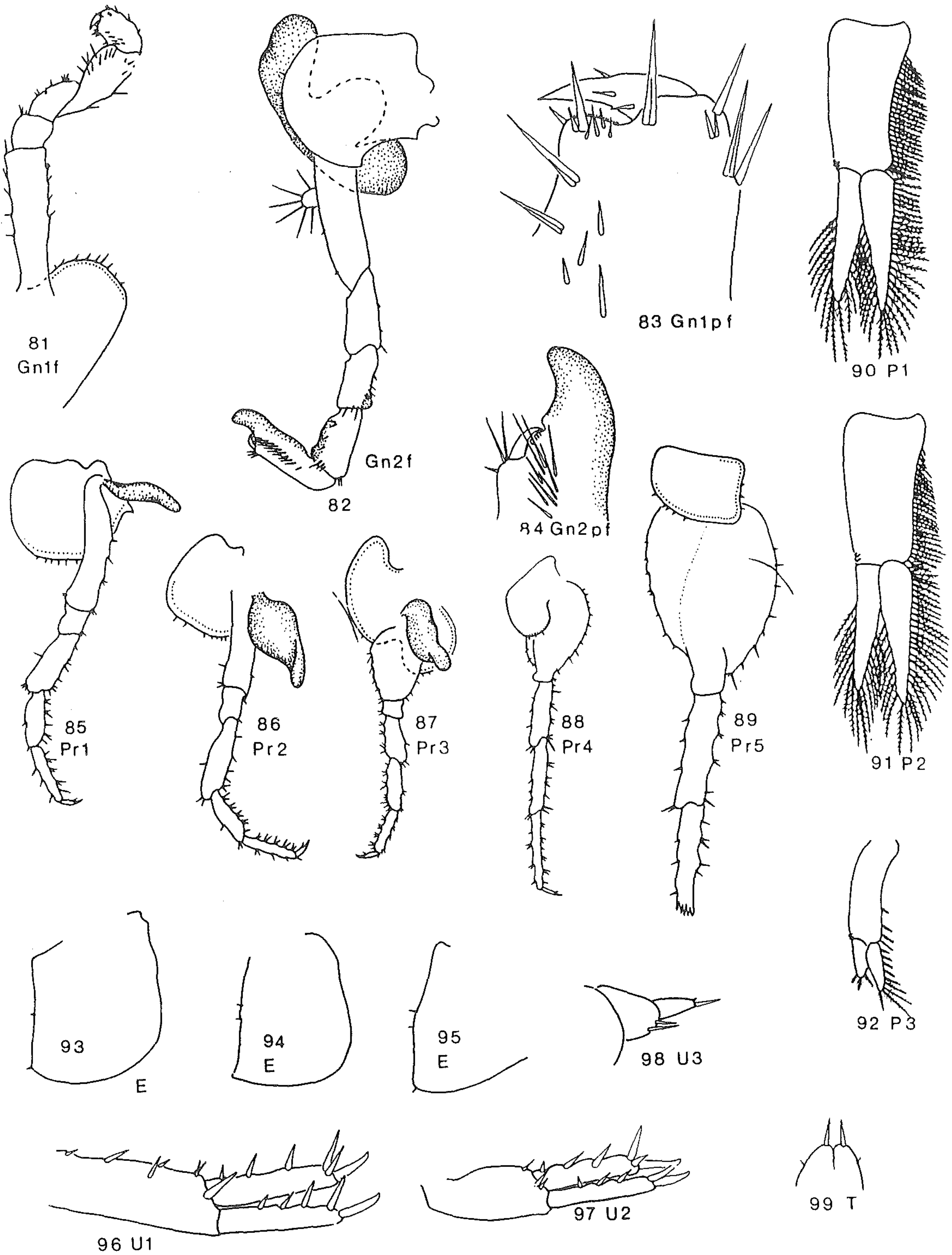


FIGURE 65. Cuticular structure of <u>Makawe hurleyi</u>. The upper micrograph shows the dorsal abdominal surface, with mesopores arranged close to the posterior border of the cuticular polygons, 'verandas' appear to overhang these pores. The lower micrograph shows a more ventral aspect; here there are two types of macropores: one opening between the boundaries of normal cuticular polygons, and one opening in a special dermal cell. The polygons formed by the dermal cells are much smaller than those formed by normal epidermal cells. The scale bar calibration is incorrect, it should read 8 micrometres.



FIGURES 66-80 Makawe hurleyi. 66, antenna 1 distal. 67, antenna 1. 68, antenna 2 distal. 69, upper lip. 70, antenna 2. 71, maxilla 2. 72, mandible. 73, maxilla 1. 74, maxilla 1 palp. 75, maxilliped. 76, lower lip. 77, gnathopod 1 male. 78, gnathopod 1 male propod. 79, gnathopod 2 male propod. 80, gnathopod 2 male.



FIGURES 81–99. Makawe hurleyi. 81, gnathopod 1 female. 82, gnathopod 2 female. 83, gnathopod 1 female propod. 84, gnathopod 2 female propod. 85, peraeopod 1. 86, peraeopod 2. 87, peraeopod 3. 88, peraeopod 4. 89, peraeopod 5. 90, pleopod 1. 91, pleopod 2. 92, pleopod 3. 93, epimeral plate 1. 94, epimeral plate 2. 95, epimeral plate 3. 96, uropod 1. 97, uropod 2. 98, uropod 3. 99, telson.

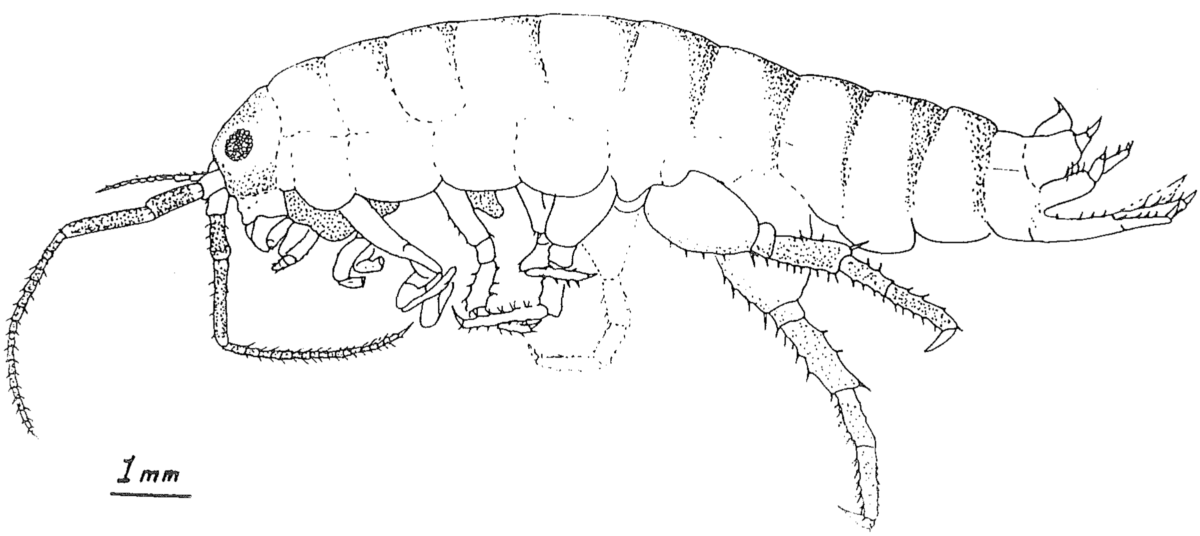


FIGURE 100. Lateral aspect of Makawe hurleyi showing pigmentation pattern in alcohol.

station. Port Levy, upper valley, Banks Peninsula, P.M.J. 30/IX/1977, *Fuchsia-Melicytus* litter. Mt.Fitzgerald Scenic Reserve MC:NZ, M.C.Crawley, 1/IX/1977, litter in relict totara forest. Ashley Gorge, Canterbury, 30/VIII/1967, in broadleaf litter. Bluff, Southland, R.R.Forster, 27/II/1940, in leafmould. Road side above Lee Stream, Outram-Hindon Rd., Otago, C.L.W., 28/XII/1965. Ross Creek, Dunedin, J.I.Sutherland, 29/I/1966, ex slit in *Fuchsia* trunk approximately 1 m above ground. Port Chalmers-Long Beach Rd., 308 m above Deborah Bay, Otago, C.L.W., 5/VI/1966. Blue Mts., Whiskey Gulley, Otago, J.Sutherland, 26.2.1966, ex beech. Chatham Islands, NZMS 240 872 920, R.Rowe, 13/II/1980, ex log. Akaroa Domain, Banks Peninsula, K.W.D., 29/III/1969. Warren St., Reserve, Oamaru, K.W.D., 6/V/1983, under *Phormium*. Leith Saddle, Dunedin district, K.W.D., 6/V/1983. Purakaunui Falls, 15 km S.W.of Owaka, Catlins district, S.Otago, G.Kuschel, 15.I.1975, sifted litter and rotten wood, 2 specimens in a large collection of 5 species.

I have also found this species widespread throughout suburban gardens and urban long grass habitats in Christchurch, Timaru, Oamaru, and Dunedin.

Etymology: The specific epithet is named for Dr D.E.Hurley in recognition of his major contributions to the study of the Amphipoda.

Diagnosis:

A large landhopper of the genus *Makawe*, pigmentation pattern consists of dark bands or 'hoops' running parallel with the segment boundaries; eyes black, round; antenna 1 short but reaching to the end of the penultimate segment on the antenna 2 peduncle, flagellum of 8 segments; antenna 2 short, of ca. 20 segments; gnathopod 1 strongly chelate in male, chelate in female; gnathopod 2 mitten-shaped in both sexes although that of the male is broader; gills simple sacs; pleopods all present, biramous with pilose setae on peduncle outer margins, pleopod 3 somewhat reduced; uropod 1 with an inter-ramal spur, both rami spined on their dorsal margins; uropod 2 both rami spined dorsally; telson with a single long spine on each lobe.

Description:

Male:

Length 10 mm; width 2.5 mm; depth 2 mm. Colour in life brownish-red background with darker brown annulations, males with a patch of brown (red in spirits) on segments 5 and 6 of gnathopod 1. Colour in spirits: background of yellowish-white with red transverse annulations. Eye black, round, diameter (0.035 mm) 0.33 head length. Cheek anterior margin has two prominent spines.

Antenna 1: length 1.4 mm, extends to end of penultimate segment of antenna 2 peduncle; peduncle segments of much same length and narrowing successively; segment 1 with small spines at 0.5 on each margin; all segments with spines at superodistal angles, the outer spines the largest; flagellum of 8 segments, all (except the first) with a group of 3-4 spines superiorly and with spines at outer superodistal angles; last segment with tuft of 4 or more setae.

Antenna 2: length 5.5 mm; peduncle 2.5 mm; segments successively narrower; 3rd segment half length of 4th, inferodistal margin fringed with 4 spines, outer with 3; 4th segment half length 5th, 4 to 6 spines along outer margin, 2 to 4 spines on inner margin; 5th segment, 5 groups of 2 spines on each margin; flagellum, varies from 6 to 23 (20 segments in type); segments subsquare in cross-section with spines at each of the four distal corners of all but the first segment; last segment tufted with 8 to 12 setae. Mouthparts: upper lip: ventral margin rounded, fringed with numerous fine setae. Mandible: upper article has 4 teeth, lower has 3; spine row of 4 plumose spines; molar area has rosette of 4 or more plumose spines distally, 1 longer plumose spine proximally. Lower lip: ventral margins and surface clothed in setae. Maxilla 1: anterior face and margins clothed with patches of very fine setae, outer ramus with minute, 2-segmented palp lightly clothed with setae, 9 serrated spines distally. Maxilla 2: margins of plates fringed with fine setae; terminal spine row double, 16 to 18 spines on outer lobe, 24 on inner, the inner row terminates in 2 plumose spines in male, 1 in female. Maxilliped: inner plate has plumose spines in 2 rows set back from the margin and arranged outside and between teeth, a single row continuing down midline cleft to basos. Outer plate a little narrower: a row of spines terminating proximally one-third down inner margin, distally with plumose spines; group of 2 to 3 spines halfway down plate. Basos distal margin spined; outer distal angles of segments from basos to propod spined; ischium with 3 spines at angle of outer lobe; carpus to propod have one spine on inner margins distally; merus to propod all have a group of spines near the mid-distal margin; propod distal margin has a few strong spines; dactylos small, not masked by propod spines.

Gnathopod 1: subchelate; coxal plate ellipsoid; ventral and posterior margins with a few very small spines; basos, width one-third length; spines on posterior margin stronger than anterior; ischium small, subrectangular; anterior margin three-quarters length posterior, spines only on posterodistal angle; merus posterior margin 1.5 times length of segment 3; posterior and distal margin spined; carpus twice length of merus, width half length; posterior margin has spine rows protecting a short row of spines at distal margin; propod sub-rectangular; posterior margin about half length of carpus, produced to a transparent scabrous area protected by row of 3 to 5 spines; anterior margin has 3 groups of 1 to 2 spines; distal angle has group of spines; palm half width of propod, transverse, partially obscured by row of stout spines, has numerous short scabrous spines; Dactylos finger projects beyond palm, 2 short spines at base of finger.

Gnathopod 2: feebly chelate; coxal plate depth = length; angles and ventral margin rounded, posterior margin excavated; gill large and lobed; basos width 0.33 length; few small spines on margins; ischium width 0.33 length; spines on posterodistal angle; merus length 0.75 ischium; posterodistal margin and angle spined; carpus widest distally; posterior margin produced to scabrous lobe which widens distally, protected by row of stout spines; propod as long as carpus; posterior margin and angle produced to scabrous lobe, protected by 2 rows of prominent spines set back from the margin; palm oblique, 0.33 width of propod, several small strong spines obscured by fringing row of stouter spines; anterodistal angle spined; dactylos short; tip fits into socket in propod lobe.

Peraeopod 1: as long as peraeopod 2; gill simple, sac-like; coxal plate ventral margin rounded and spined; posterior margin excavated, spined; deeper in female than male; basos widening distally; spined marginally and at angles; length 5 times width; subrectangular, as long as wide; distal angles spined; merus margins spined, posterior spines the largest; carpus width 0.33 length 0.5 merus width; posterior margin with prominent spines; anterior with group of small spines at 0.5 and at distal angle; propod width 0.15, length 0.5 segment 5 width; posterior margin has 5 groups of spines, anterior has 3 groups; distal angles spined; Dactylos notching not pronounced; one spine on each margin.

Peraeopod 3: slightly longer than first and second; sideplate longer than deep, deeper in female, otherwise like peraeopod 1; gill simple larger than in peraeopod 2; basos posterior margin with pairs of short and long spines; anterior with long spines only merus expands distally; ischium and merus shorter than in peraeopod 1 and 2, other segments longer.

Peraeopod 4: sideplate ventral margin spined, slightly crenulated; gill large with two lobes; basos width 0.75 length, strong single spines on margins; other segments longer than in peraeopod 3.

Peraeopod 5: sideplate longer than deep (deeper in female); margins spined; posterior slightly excavated; posterior angle acute; basos nearly as wide as long; merus to propod successively narrower and longer; dactylos long and narrow, only 1 spine in axilla.

Epimeral Plates: subtriangular; posterior angle acute but rounded; small spine half-way up posterior margin. Second: subsquare; anterior angle and ventral margin rounded; posterior margin slightly excavated, small spine at 0.75. Third: squarer than second, ventral margin less rounded; anterior margin slightly sinuous; small spines at posterior angle and half up posterior margin.

Pleopods: segmentation of rami only superficial. First: inner ramus slightly smaller than outer; setulose spines down outer margin of base and all margins of rami; rami longer than peduncle; all margins fringed with very fine setae; two coupling spines at peduncle inner distal angle. Second: longer than first; spination similar; inner ramus only slightly smaller than outer. Third: length 0.5 second; reduced but still biramous; inner ramus two-thirds length outer; setulose setae only on distal half of peduncle outer edge; inner edge has two coupling spines; outer edge of outer rami with only 7 or so setulose spines, inner edge has even fewer; outer ramus very sparsely spined. Male: spination reduced even more than in female; outer margin of peduncle with 2 spines; outer ramus, 3 spines; inner ramus, 1 spine.

Uropod: peduncle as long as rami; male, 4 spines on each dorsal margin; female with 5; large inter-ramal spine present, its length one-third rami; outer ramus with 3 spines dorsally, 1 long (hooked) and 2 short terminally; inner with 4 spines dorsally, 2 long (hooked) and 2 short terminally. Second: peduncle with 4 spines on outer dorsal margin, 2 smaller spines on inner dorsal margin; outer ramus with 2 spines dorsally, 2 long and 2 short terminally; inner ramus with 3 dorsally, 2 long and 2 shorter terminally. Third: small peduncle as long as ramus; has 2 spines; ramus has 1 terminally. Telson: moderately cleft, subtriangular, 1 spine on end of each lobe.

Female:

Length 12 mm; width 3 mm; depth 2 mm. Antenna 1: length 1.27 mm; 3rd peduncle segment with 2 spines at each superodistal angle; flagellum of 6 segments. Antenna 2: length 4.8 mm; flagellum length 2.7 mm, number of segments varies from 6 to 22 (18 in allotype). Gnathopod 2: sideplate deeper than long, spines more numerous than in male; broodplate length 5 times width; ends in 9 spines, each longer than width; basos, anterior margin only spined; merus posterior margin produced into scabrous lobe; spines down posterior margin and at distal angle; carpus, posterior and distal margin spined, produced in scabrous lobe; palm of propod more oblique than male; dactylos relatively shorter.

Coxal plates deeper than in male.

Pleopod 3 spination not as reduced as in male.

Remarks

Makawe hurleyi is commonly found in South Island and the Chatham Islands where it inhabits temperate and alpine grasslands, damaged native forest and ecotones of less damaged forests. Wildish (1979) has incorrectly recorded this species as occurring in tropical grasslands. It also occurs in adventive communities such as: exotic pine forests, in the leaf litter under exotic angiosperm trees and shrubs, and in suburban gardens and waste grassland in southern urban areas of New Zealand. In fact, it is present wherever it is damp enough in grasslands or man-induced habitats in Canterbury and Otago. It is usually abundant where it occurs. It is easily recognised by its uropod spination and pigmentation pattern.

No other landhopper seems to have invaded grassland so thoroughly as has this species. In coastal Otago and Southland, _Talorchestia patersoni_ does to a certain extent, but it does not penetrate inland very far. Grass litter is very abrasive since it contains silicon, and this coupled with the toxins present in grass may account for the absence of other landhoppers from the grassland environment. Much of the original vegetation in Canterbury and Otago consisted of wide expanses of tussock grassland of the pampas-grass type which produced a comparatively thick litter and a well-buffered microenvironment beneath a tall canopy. These conditions were possibly conducive to the evolution of a grassland form.

Makawe waihekensis new species

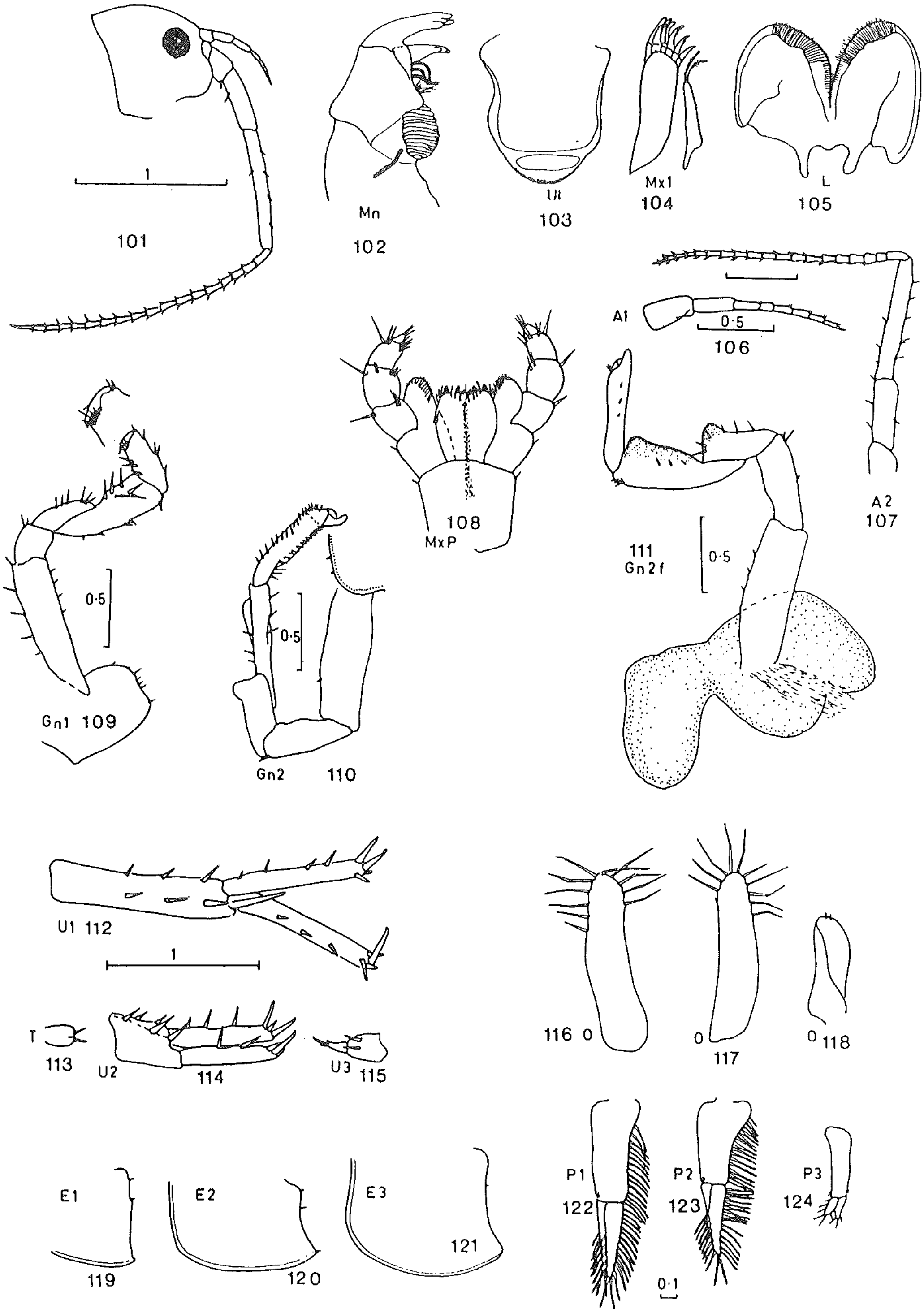
Figures 101 to 125

Types: Holotype male: Waiheke Island, Auckland, 12/II/1949, G.Chamberlain, deposited in the Canterbury Museum (slide and tube containing dissected remains). (Author's catalogue no. KD 630). An allotype female from same collection, has also been deposited in the Canterbury Museum. The types were taken with 1 other male and 3 other females of the same species plus one *Parorchestia tenuis*. All the females were in breeding condition and one was ovigerous.

Etymology: named after the type locality which means 'ebbing water' in Maori (Reed and Brougham, 1978).

Diagnosis:

A small, weakly sexually dimorphic landhopper of the genus *Makawe*, eyes large, deeply pigmented; antenna short, does not reach to the beginning of the last segment of the antenna 2 peduncle; antenna 2 moderately long; both antennae have very short spines; gnathopod 1 without a plinthic ridge, propod chelate in both sexes; gnathopod 2 propod mitten-shaped in both sexes; gills moderately large but of a simple discoidal shape and are half-spiralled except for first and last which are lobed; pleopods all present, biramous, the last reduced in size, peduncle outer margins setose, rami heavily setose; uropod 1 has a long inter-ramal spur, both rami weakly spined dorsally; uropod 2 rami both spined; epimeral plates all subsquare, anterodistal angles rounded.



FIGURES 101-124. Makawe waihekensis. 101, cephalon. 102, mandible. 103, upper lip. 104, maxilla 1. 105, lower lip. 106, antenna 1. 107, antenna 2. 108, maxilliped. 109, gnathopod 1 male. 110, gnathopod 2 male. 111, gnathopod 2 female. 112, uropod 1. 113, telson. 114, uropod 2. 115, uropod 3. 116, oostegite 1. 117, oostegite 2. 118, oostegite 4. 119, epimeral plate 1. 120, epimeral plate 2. 121, epimeral plate 3. 122, pleopod 1. 123, pleopod 2. 124, pleopod 3.

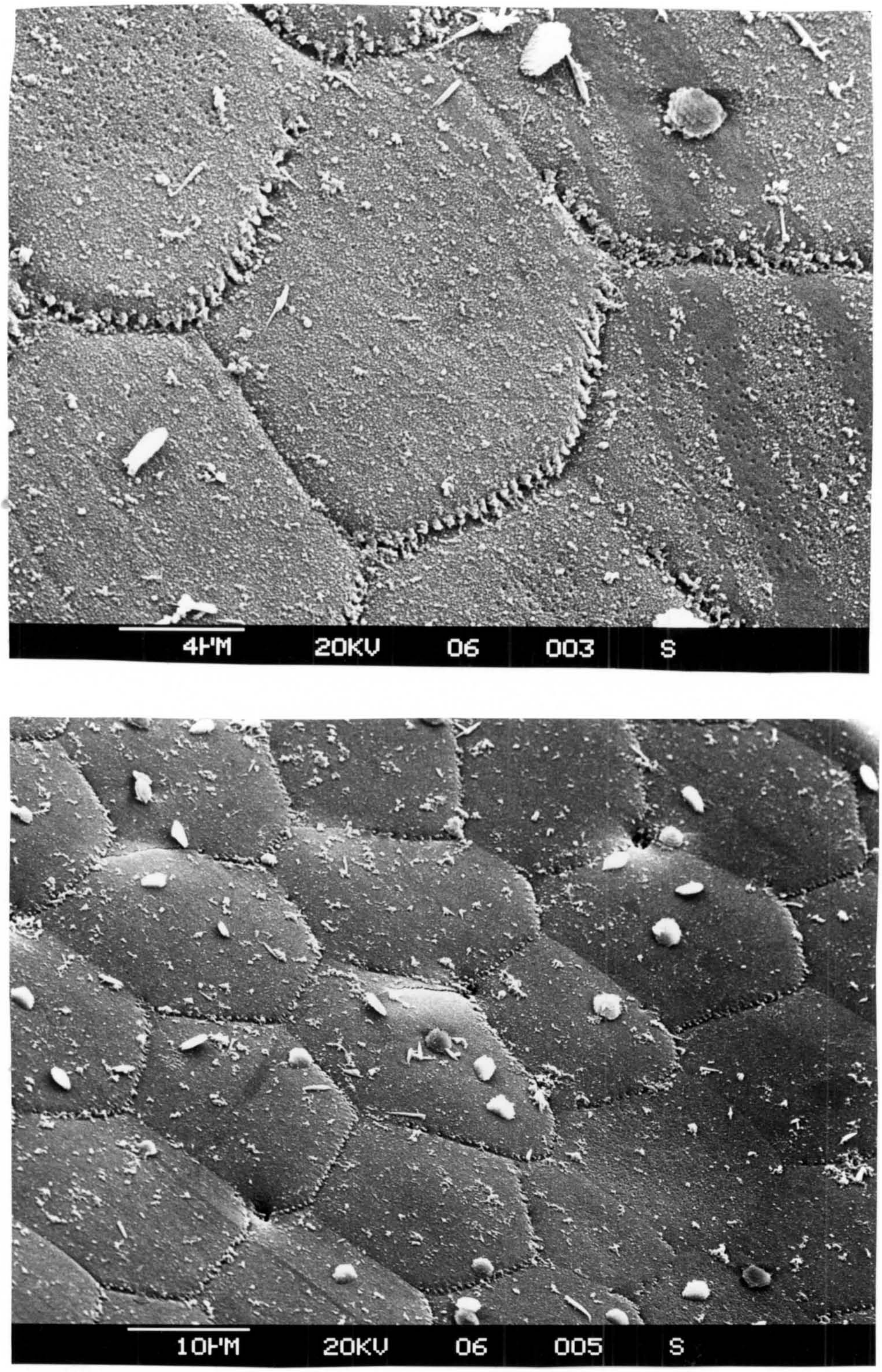


FIGURE 125. Cuticular structure of Makawe waihekensis. Note the close similarity to M.hurleyi.

Description:

Male:

Length 11.2 mm, width 2.17 mm, depth 2.35 mm. Pigmentation pattern unknown. Eye dark, diameter about 0.33 head capsule length. Antenna 1: does not reach the beginning of antenna 2 peduncle last segment; length 1.36 mm; peduncle segment 1 lost; segment 2 with a minute spine at the interodistal angle; segment 3 narrow, with a minute spine at inferodistal angle; flagellum of 7 segments, each about same length, each with a group of minute spines superodistally, terminal segment short with a rudimentary terminal tuft. Antenna 2: length 6.55 mm; peduncle length 2.90 mm, peduncle segment 3 with a group of 3 longer spines at inferodistal angle; segment 4 superior margin spined at 0.40, inferior margin spined at 0.17 and 0.54 (2), inferodistal angle with 1 spine; segment 5 narrowing slightly distally, long, superior margin spined at 0.20, 0.33, 0.53, 0.67, and 0.79, inferior margin spined at 0.15, 0.27, and 0.48; flagellum moderately long and slender, tapering, of 20 podomere segments, each segment has short spines at each of the 4 distal angles; terminal tuft very short and tight.

Mouthparts: upper lip: distal margin slightly more pointed than usual, densely pilose, inner shelf present. Mandible: incisor 5-toothed, lacinia mobilis with 4 teeth arranged in a plane, 4 interdentate pilose setae, abmolar setal tuft dense; molar 15 striate; molar medial seta present and densely pilose, length equal to molar width. Maxilla 1: outer plate broadening slightly distally; distal margin with 8 spines bearing 0, 0, 1, 3, 4, 4, 4, 0 lateral teeth; inner plate narrowing distally, terminating in 2 pilose setae, inner margin finely pilose. Maxilla 2: outer plate ellipsoid, distal margin rounded with numerous inwardly curved spines, outer margin pilose; inner plate distally pointed, distal margin flanked by a spine row which terminates proximally with 1 long, pilose seta, inner margin pilose. Lower lip: scroll-shaped, inner and distal margin heavily pilose. Maxilliped: moderately broad; inner plate rounded distally, with 2 large and 1 small spine teeth, below and beyond these is a row of pilose setae which extend distally beyond them; outer plate inner margin nearly straight with a setal comb set back from distal and inner margins; palp segments 1, 2, and 3 with 1 long spine at outer distal angle and a spine tuft at inner distal angle; palp segments 2 and 3 distal margins spined; palp segment 4 present, spined, not obscured by segment 3.

Gnathopod 1: coxal plate antero- and posterodistal angles rounded, distal margin slightly emarginate, with 9 spines; plinthic ridge not present; basos broadening distally, anterior margin straight, spined at 0.62, 0.75, 0.85, 0.95, and 0.97, posterior margin convex, scalloped, with large spines at 0.26, 0.39, 0.59, and 0.79, posterodistal angle with 1 spine; ischium anterior margin sinuous, slightly produced distally, posterodistal angle with 2 spines; merus posterior margin convex, spined at 0.34, 0.44, 0.53, 0.61 (2), 0.76, 0.81, 0.84, 0.87, and 0.89; carpus broadening distally, anterior margin stepped, spined at 0.20, 0.33, 0.58, 0.64, and 0.92 (1+2), posterior margin spined at 0.24, 0.41, and 0.59, posterodistal angle with 1 spine; propod narrower than carpus, anterior margin stepped and scalloped, spined at 0.32, 0.55 (3), and

0.80 (2), anterodistal angle with 2 spines; posterior margin sinuous being emarginate distally, spined at 0.40, 0.55, and 0.73, palm convex, 0.5 propod width, flanked by a row of 6 spines, palmar angle about 97°; dactyl projects beyond propod margin, with 1 spine on outer (anterior) margin at base of terminal spine.

Gnathopod 2: distorted in type; basos narrowing slightly distally, anterior margin with a small spine at 0.71, posterior margin slightly sinuous, naked; ischium broadening distally, anterior margin slightly produced into a very discrete pellucid lobe distally; propod long, mitten-shaped, with many spines running in longitudinal rows on both faces, palm oblique, small; dactyl small.

Peraeopod 1: gill moderately large, simple, narrowing distally; basos curved slightly anteriorly, anterior margin with spines at 0.64, 0.75, and 0.91, posterior margin with spines at 0.40, 0.52, and 0.80, posterodistal angle with 2 spines; ischium with 1 large and 1 minute spine at posterodistal angle; merus broadening slightly distally, posterior margin spined at 0.21, 0.44, and 0.72, posterodistal angle with 2 spines; carpus anterior margin stepped, spined at 0.56, anterodistal angle with 1 spine, posterior margin scalloped, spined at 0.18 (2), 0.39 (2), 0.63 (2), and 0.75 (3), posterodistal angle with 1 spine; propod narrowing slightly distally, anterior margin stepped and slightly scalloped, spined at 0.23 (2), 0.52 (2), and 0.79 (2), posterodistal angle with 2 spines, posterior margin scalloped, spined at 0.11 (1), 0.19 (2+1), 0.36 (2+1), 0.52 (2+1), 0.70 (2+1), and 0.87 (2+1); dactyl curved inwardly, somewhat wasp-waisted due to margins being slightly emarginate distally.

Peraeopod 2: gill simple but distal half is 1/4 turned; coxal plate ventral margin almost straight, slightly emarginate, with 6 small spines; basos margins subparallel, anterodistal angle with 1 spine, posterior margin spined at 0.50 and 0.69; ischium anterior margin not produced, posterodistal angle with 1 spine; merus broadening distally, posterior margin spined at 0.18 and 0.44, posterodistal angle with 2 spines; carpus anterior margin slightly stepped and spined at 0.51 and 0.77, anterodistal angle with 1 spine, posterior margin scalloped, spined at 0.15, 0.41 (2), and 0.77 (4); propod broadest medially, anterior margin stepped, spined at 0.26, 0.45, and 0.77, anterodistal angle with 2 spines, posterior margin scalloped, spined at 0.19 (2+1), 0.33 (2+1), 0.52 (2+1), 0.68 (2+1), and 0.86 (2+1).

Peraeopod 3: coxal plate ventral margin rounded, with 2 minute spines; basos an inverted pyriform shape; anterior margin nearly straight distally, scalloped, spined at 0.18, 0.28, 0.37, 0.49, 0.61, 0.76, and 0.88, anterodistal angle with 1 spine, posterior margin stepped, spined at 0.16, 0.31, 0.41, 0.53, 0.72, 0.90, and 0.96; ischium anterodistal angle with 1 spine; merus broadening distally, anterior margin scalloped, spined at 0.22 (2), 0.49 (2), and 0.82 (1), anterodistal angle with 2 spines, posterior margin stepped, spined at 0.45, posterodistal angle with 1+1 spine; carpus margins subparallel, anterior margin scalloped, spined at 0.21 (1), 0.34 (3), 0.58 (3), and 0.89 (3), posterior margin stepped and slightly scalloped, spined at 0.42 (1), and 0.67 (1+1), posterodistal angle with 1 larger and 1 smaller spine; propod narrowing slightly distally, anterior margin scalloped, spined at

0.12 (1), 0.22 (2), 0.40 (3), 0.63 (3), and 0.85 (3), posterior margin stepped, spined at 0.33 (2), 0.58 (2), and 0.78 (2), posterodistal angle with 2 spines; dactyl wasp-waisted, inner margin with 1 large spine at base of terminal spine.

Peraeopod 4: gill broad with relatively short, triangular pendulous lobe; basos ovoid, width 0.56 length, anterior margin with larger spines at 0.06, 0.17, 0.27, 0.32, 0.44, 0.54, 0.69, and 0.83, anterodistal angle with 1 spine, posterior margin slightly stepped, with small spines at 0.45, 0.61, 0.74 and 0.87; ischium anterodistal angle with 2 spines; merus broadening slightly distally, anterior margin scalloped, spined at 0.13 (1), 0.25 (1), 0.45 (3), 0.67 (3), and 0.90 (2), anterodistal angle with 1 long spine, posterior margin stepped, spined at 0.26 and 0.53, posterodistal angle with 2 spines; carpus long, margins subparallel, anterior margin scalloped, spined at 0.17 (1), 0.29 (2), 0.53 (2), 0.73 (1), and 0.89 (2), posterior margin nearly straight, spined at 0.32, 0.48, and 0.70, posterodistal angle with 4 spines; propod long, anterior margin spined at 0.16 (1), 0.29 (2), 0.52 (2), 0.65 (3), 0.74 (2), and 0.90 (2), posterior margin spined at 0.21 (2), 0.38 (3), 0.62 (3), 0.77 (2), and 0.90 (2); dactyl slightly wasp-waisted.

Peraeopod 5: basos width 0.77 length; anterior margin slightly stepped, with large spines at 0.15, 0.23, 0.35, 0.50, 0.63, 0.74, and 0.89, posterior margin scalloped, with minute spines at 0.20, 0.29, 0.35, 0.45, 0.53, 0.64, 0.73, 0.80, and 0.91, posterodistal angle with 2 spines; ischium anterodistal angle with 2 spines; merus anterior margin scalloped, spined at 0.12 (1), 0.25

(2), 0.44 (3), and 0.69 (2), anterodistal angle with 2 spines, posterior margin with small steps, spined at 0.26 and 0.54, posterodistal angle with 2 spines; carpus margins subparallel, anterior margin deeply scalloped, spined at 0.15 (2), 0.28 (1), 0.45 (3), 0.64 (3), 0.79 (1), and 0.85 (1), posterior margin scalloped, spined at 0.26, 0.43, and 0.67; propod both margins stepped, anterior margin spined at 0.10 (2), 0.21 (2), 0.35 (3), 0.45 (2), 0.56 (3), 0.69 (2), 0.75 (2), 0.84 (2), and 0.91 (2), posterior margin spined at 0.18 (1), 0.29 (3), 0.46 (2), 0.67 (3), 0.84 (1), and 0.92 (2), posterodistal angle with 2 spines; dactyl only slightly wasp-waisted, both margins sinuous.

Pleopods: all are comparatively broad and stout. Pleopod 1: length 1.20 mm, peduncle outer margin heavily setose with pilose setae, inner margin naked except for 2 coupling spines distally; inner ramus slightly shorter than outer, both with long pilose setae on inner and outer margins. Pleopod 2: length 1.02 mm otherwise as for first. Pleopod 3: reduced but still biramous, length 0.60 mm, 2 coupling spines present on peduncle inner margin; both rami equal in length, with a few short pilose setae.

Epimeral plate 1: subtriangular, posterodistal angle notched, posterior margin with 2 small, backward-pointing spines proximally . Epimeral plate 2: anterodistal angle rounded, ventral margin convex, posterodistal angle acute, with a minute spines, distal margin convex, with 2 small spines proximally, emarginate distally. Epimeral plate 3: ventral margin more rounded than second, posterodistal angle acute and rounded apically, posterior margin emarginate, with 1 spine proximally.

Uropod 1: peduncle with a row of 3 spines and another of 2 spines dorsally, a large inter-ramal spur is present extending about 0.33 length of rami; outer ramus with 2 spines dorsally, inner ramus with 4 spines dorsally, both rami terminate with 2 larger and 2 smaller spines. Uropod 2: peduncle with 1 spine dorsally, a large inter-ramal spur extends about 0.25 length of rami; both ramus with 3 spines dorsally and 1 long, 2 slightly smaller and 2 small spines terminally. Uropod 3: uniramate; peduncle with 2 dorsal spines; ramus with no marginal spines, terminates with 1 larger and 1 smaller spine. Telson not cleft, 1 marginal spine directed posteriorly on each lobe.

Female: as for male except where specified.

Length 10.75 mm; width 2.59 mm; depth 2.94 mm; Antenna 1: peduncle segment 1 short, with 1 minute spine at inferodistal angle; flagellum of 6 segments; the first segment is the longest. Antenna 2: segment 4 dorsal margin naked.

Mouthparts: Maxilla 1 outer plate with a small palp present on outer margin.

Gnathopod 1: ischium posterior margin with 1 spine at 0.50; carpus anterior margin with only 3 spine groups; propod slightly narrower than in male.

Gnathopod 2: gill broad, trilobed with a large subcephalic lobe; basos anterior margin spined at 0.34, 0.47, 0.59, and 0.73, posterior margin naked; ischium posterior margin with 1 small spine midway, posterodistal angle with 4 spines; merus posterior margin produced distally into a discrete pellucid lobe, margin has about 8 longer spines; carpus anterior margin convex, naked, anterodistal angle with 3 spines, posterior margin produced into a pellucid lobe, which is widest distally, with a few spines along the base of the lobe; propod shorter than carpus, palm short, oblique, flanked by a few spines; palmar angle about 50^{o}, propod posterior margin produced into a pellucid lobe which extends beyond the palm, a row of spines runs longitudinally along face.

Brood plates: all except last pair with rounded distal end bearing about 11 setae; last pair have a margin rolled, distal end bears 2 vestigial setae.

Uropod 1: peduncle with 3 spines in each dorsal row; outer ramus with 3 spines dorsally. Uropod 2: peduncle with 4 spines dorsally; outer ramus with 2 dorsal spines.

Remarks

It was with some reluctance that I described this species from the material available since the specimens had deteriorated a little from their long storage in alcohol. But because they belong to a good species, and as no other material is available I feel justified in describing it using the specimens at hand.

It is very similar to M.hurleyi from the South Island; so similar, in fact, that it can be regarded as a sibling species differing only in the smaller size, the more reduced pleopod 3, the reduced spination on the dorsal margin of uropod 1, the shorter first antenna, and the emarginate epimeral plate posterior margin.

It is easily separated from most other Northland and Auckland landhoppers by having both rami of uropod 1 spined dorsally, a character seen only in the genus Tara amongst the other Auckland species. Its pigmentation pattern is unknown but, if it is a M.hurleyi sibling species, it probably has the same pattern of diffuse red hoops running around the body as does M.hurleyi. The gills, however, are larger than those of M.hurleyi. Presumably, this is because of the warmer environmental temperatures it experiences which means that less oxygen can dissolve per unit volume of fluid bathing the gills. Hence larger gills are required to maintain an adequate rate of oxygen uptake.

Interestingly, M.hurleyi is a dominant catastrophe-community and grassland species penetrating damaged and arid environments, achieving very high densities, and thriving in man-made habitats. Yet M.waihekensis, which is so similar morphologically, appears to be relict occuring only on Waiheke Island. It may be more widespread than this, but it cannot be a dominant species since it would have been detected by me in some of the thousands of collections I have examined from Northland and Auckland provinces. Obviously, morphology alone does not explain dominance or rareness in landhoppers.

Makawe otamatuakeke new species

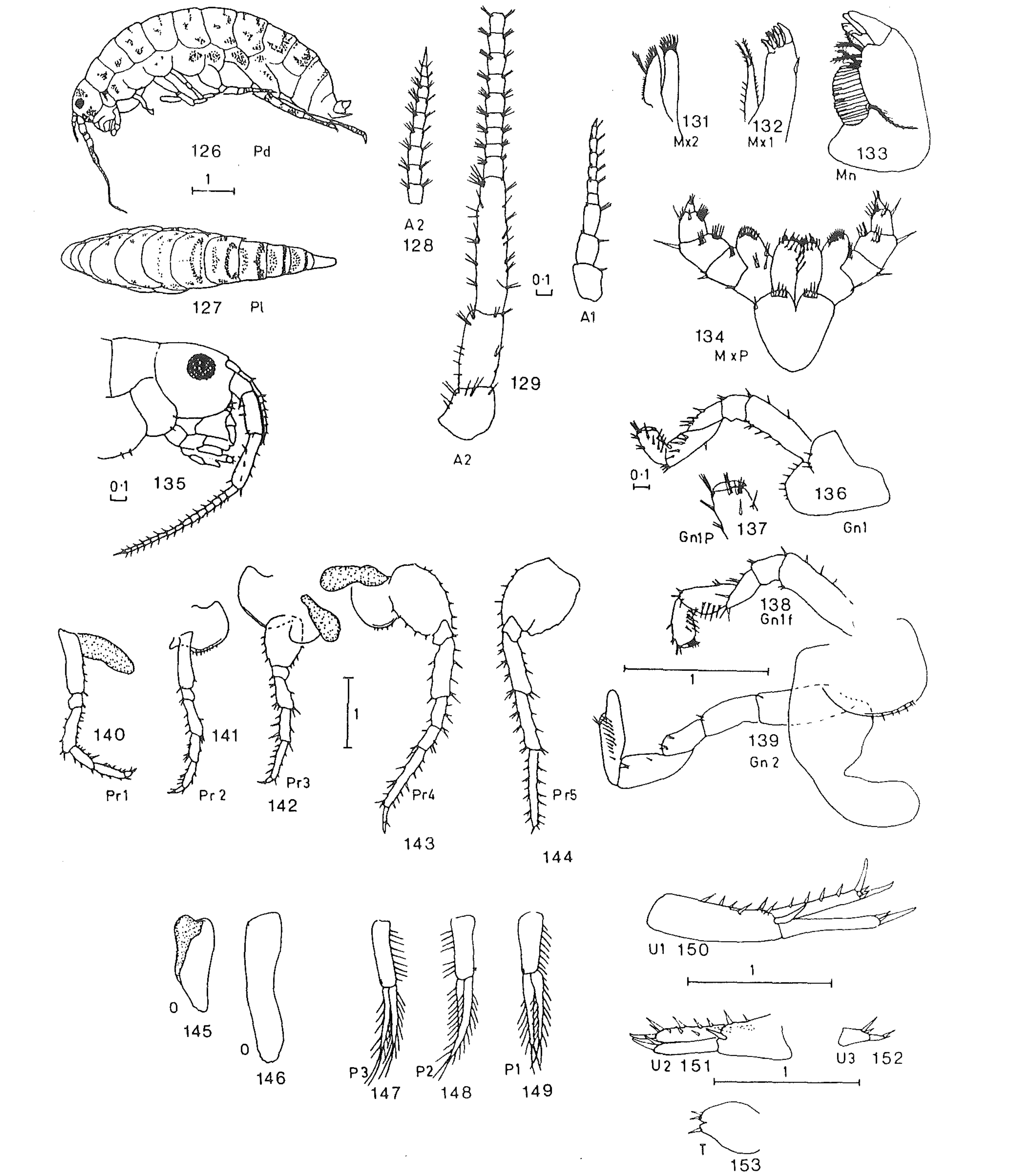
Figures 126 to 154

Types: the male holotype and female allotype were collected at Warren Street Reserve, Oamaru, South Island, New Zealand, by K.W. Duncan, 6.V.1983, and deposited in the Canterbury Museum, (slides and tube containing dissected remains). They were collected along with *Talorchestia patersoni*, *M.hurleyi*, and *Parorchestia ihurawao*.

Etymology: from the Maori word meaning 'from my Uncle's place'. This name was given because the type was collected from Mr Arthur Lawson's (my wife's uncle) garden which borders the reserve in which the species is abundant.

Diagnosis:

A moderate sized landhopper of the genus *Makawe*; the body pigmentation pattern in alcohol consists of transverse reddish hoops superolaterally and dots laterally; eyes round, black; antenna 1 short, extends to or just beyond junction of antenna 2 peduncle segments 4 and 5; antenna 2 short, not very tapering, delicately spined; gnathopod 1 chelate in both sexes; gnathopod 2 mitten-shaped in both sexes; peraeopods not very long and not particularly stout; pleopods all present and biramous, outer margins of peduncles setose; uropod 1 outer ramus naked, with a smaller inter-ramal spur; uropod 2 outer ramus naked, inner ramus with 2 rows of marginal spines dorsally; telson moderately cleft.



FIGURES 126-153. Makawe otamatuakeke. 126, lateral aspect. 127, dorsal aspect. 128, antenna 2 distal. 129, antenna 2 proximal. 130, antenna 1. 131, maxilla 2. 132, maxilla 1. 133, mandible. 134, maxilliped. 135, cephalon. 136, gnathopod 1 male. 137, gnathopod 1 male propod. 138, gnathopod 1 female. 139, gnathopod 2 male. 140, peraeopod 1. 141, peraeopod 2. 142, peraeopod 3. 143, peraeopod 4. 144, peraeopod 5. 145, oostegite 4. 146, oostegite 1. 147, pleopod 3. 148, pleopod 2. 149, pleopod 1. 150, uropod 1. 151, uropod 2. 152, uropod 3. 153, telson.

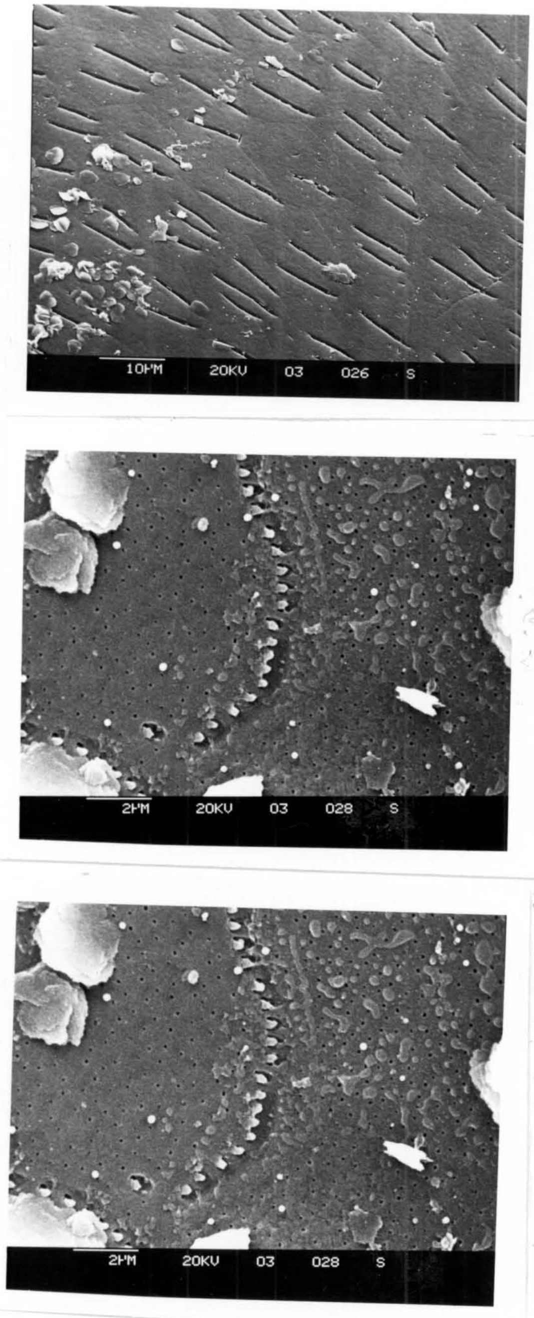


FIGURE 154. Cuticular structure of Makawe otamatuakeke. The upper micrograph shows the dorsal surface of abdominal segment 2. Here the mesopores are located in slits directed posteriorly. The slits are formed into arcs on the posterior margins of the cuticular polygons (not well shown). The middle micrograph is from the lateral aspect of the same abdominal segment. The slits are shorter and are more definitely arranged in arcs. The lower micrograph is from a more ventral aspect of the same abdominal segment and shows the slits to be very short with the mesopores arranged in arcs near the posterior borders of the cuticular polygons. The material projecting from the pores is most likely mucoid.

Description:

Male:

Length 10.9 mm, width 1.50 mm, depth 1.57 mm; pigmentation pattern (in alcohol) with 1 red transverse stripe on each segment superolaterally widening into a longitudinal stripe or dot laterally, sideplates with a large, diffuse red spot, appendages transversely banded. Eyes black, round, about 0.33 head capsule length. Cheek with 3 prominent setae.

Antenna 1: length 1.20 mm; extends just beyond junction of antenna 2 peduncle segments 4 and 5; peduncle longer than 7 segmented flagellum; peduncle segment 1 is longer and broader than segments 2 and 3, spined at superodistal angle; segment 2 spined on inferior margin at 0.5, supero- and inferodistal angles with 2 spines each; segment 3 as long as segment 2 but narrower, broadening distally; flagellum segments successively narrower and longer; ultimate segment short and triangular bearing a short, sparse terminal tuft.

Antenna 2: length 3.85 mm; heavily spined with long, delicate spines, flagellum tapering, of 19 segments; peduncle segment 3 spined at distal margin and on inferior margin; segment 4 1.5 length segment 3, margins convex, spined; segment 5 1.8 length segment 4, narrowing distally, margins heavily spined and scalloped.

Mouthparts: upper lip: ventral margin semi-circular, pilose, inner shelf present. Mandible: with 6 interdentate pilose setae, abmolar setal tuft prominent, molar 20 striate, molar medial seta long and pilose. Maxilla 1: outer plate broadening distally, distal margin with 9 inwardly-curved teeth, the inner 5 of which bear 4 lateral teeth; inner plate narrow, narrowing distally, both margins sparsely pilose, terminates with 2 pilose setae. Maxilla 2: outer plate narrowing slightly distally, inner plate foliaceous with the inner margin pilose. Maxilliped: broad with relatively few, although large spines; inner plate distal margin rounded with 2 large and 1 small spine teeth each, pilose setae set submarginally, continuing down midline; outer plate distal margin rounded, submarginal setal comb short, not continued down inner margin; peduncle segment 1 with a short row of stout spines on medial distal margin; peduncle outer distal angles spined; palp broad, segment 4 comparatively large, not obscured by segment 3.

Gnathopod 1: coxal plate ventral margin rounded, with 2 large and 7 smaller marginal spines; plinthic ridge with 2 spines; basos margins subparallel, curved anteriorly, anterior margin slightly concave, spined at 0.44, 0.58, and 0.71, anterodistal angle with 3 spines, posterior margin convex, with larger spines at 0.43 and 0.76, posterodistal angle with 1 spine; ischium anterior margin sinuous, posterodistal angle with 3 spines; merus posterior margin spined at 0.42, 0.62, 0.70, 0.71 (submarginal), 0.76, 0.81, and 0.86, carpus anterior margin spined at 0.35 (2), anterodistal angle with 3 spines, posterior margin with about 8 large spines in a row between the posteroproximal angle and the mediodistal margin, posterodistal angle with 1 large spine; propod moderately broad, both margins convex, anterior margin stepped and spined at 0.72 (3), and 0.84 (3), anterodistal angle with 3 long spines, posterior margin with submarginal spines at 0.17, 0.35, and 0.52, palm convex, 0.5 propod width, flanked by 2 large spines anteriorly, 5 smaller spines mesially, and 3 larger spines posteriorly, palmar angle 101°; dactyl projects beyond propod margin slightly.

Gnathopod 2: coxal plate ventral margin rounded, with about 13 spines; gill large, not convoluted, subcephalic lobe long with a rounded distal margin; basos narrowing distally, anterior margin convex, spined at 0.79, posterior margin sinuous, naked, posterodistal angle with 1 minute spine; ischium long, posterodistal angle with 1 spine; merus produced distally into a pellucid lobe guarded by 1 large spine at its proximal edge and 4 spines at its distal edge; carpus anterior margin naked, anterodistal angle with 4 spines; posterior margin produced into a pellucid lobe which is broadest distally and guarded at its base by 1 spine proximally and 3 spines distally; propod mitten-shaped, long, anterior margin sinuous, naked, anterodistal angle with 4 spines, posterior margin produced distally into a pellucid lobe which extends well beyond palmar area, palm small, oblique, flanked by 6 spines at its posterior end, palmar angle 37°; dactyl short, appears to occlude propod pellucid lobe.

Peraeopod 1: coxal plate ventral margin nearly straight; gill a simple ellipsoidal sac; basos broadening distally, both margins convex and stepped, anterior margin scalloped, spined at 0.58, 0.69, 0.85, and 0.91, posterior margin spined at 0.31, 0.50, 0.67, and 0.79, posterodistal angle with 2 spines; ischium posterodistal angle with 2 large and 1 small spine; merus broadening distally, both margins scalloped, anterior margin spined at 0.26, 0.47, and 0.72, posterior margin spined at 0.08, 0.19 (2), 0.41 (2), 0.68 (2), and 0.88, posterodistal angle with 2 spines; margins subparallel, curved posteriorly, anterior margin convex, stepped, spined at 0.33 and 0.59, anterodistal angle with 3 small spines, posterior margin with larger spines at 0.11, 0.28 (2), 0.56, 0.63, 0.70, and 0.74, posterodistal angle with 3 larger spines; propod broadest medially, both margins stepped and scalloped, anterior margin spined at 0.26 (2), 0.51 (2), and 0.82 (2), anterodistal angle with 3 spines, posterior margin spined at 0.18 (2), 0.28 (2), 0.40 (2), 0.54 (2), 0.70 (2), and 0.87 (2), posterodistal angle with 1 spine; dactyl short, conical, margins not emarginate.

Peraeopod 2: coxal plate ventral margin straight, with 10 spines; basos curved anteriorly, anterior margin spined at 0.67 and 0.78, posterior margin spined at 0.38, 0.50, 0.64, and 0.88, posterodistal angle with 2 spines; ischium posterodistal angle with 2 spines; merus broadening distally, anterior margin spined at 0.50, anterodistal angle with 3 spines, posterior margin slightly scalloped, with larger spines at 0.24 (2), 0.51 (2), and 0.76 (2), posterodistal angle with 3 spines; carpus broadening distally, anterior margin stepped, spined at 0.47, anterodistal angle with 2 spines, posterior margin scalloped and stepped, with larger spines at 0.29 (2), and 0.56 (2), posterodistal angle with 4 spines; propod curved posteriorly, anterior margin convex, stepped, spined at 0.34 (2), 0.62 (2), and 0.84 (2), anterodistal angle with 2 spines, posterior margin deeply scalloped, spined at 0.21 (2), 0.35 (2), 0.53 (2), 0.69 (1), and 0.82 (2); dactyl short, conical, curved posteriorly, posterior (inner) margin slightly emarginate.

Peraeopod 3: coxal plate lobes broadly rounded, anterior with 10 spines, posterior with 6 spines; gill is simple, flattened discoid; basos an inverted pear-shape, both margins with 8 large spines; ischium anterodistal angle with 2 spines; merus broadening distally, both margins stepped, anterior margin spined at 0.45, anterodistal angle with 4 spines, posterior margin spined at 0.13 (1), 0.29 (2), and 0.60 (2), posterodistal angle with 3 spines; carpus anterior margin stepped, spined at 0.60, anterodistal angle with 2 spines, posterior margin scalloped, spined at 0.12, 0.28, 0.52, and 0.79, posterodistal angle with 2 spines; propod narrowing distally, both margins stepped, anterior margin spined at 0.31 (2), 0.51 (2), and 0.83 (2), anterodistal angle with 3 spines, posterior margin spined at 0.16 (1), 0.27 (2), 0.41 (2), 0.61 (2), 0.77 (2), and 0.83 (1).

Peraeopod 4: coxal plate ventral margin rounded with 6 small spines; gill a simple ellipsoid; basos nearly ovate, broadest proximally, both margins spined although those on the anterior are slightly larger; ischium anterodistal angle with 2 spines; merus broadening distally, anterior margin stepped, spined at 0.12 (1), 0.21 (2), 0.35 (1), 0.44 (3), 0.64 (1), and 0.71 (2), anterodistal angle with 3 spines, posterior margin scalloped, spined at 0.14, 0.30, and 0.62; carpus damaged in type; propod narrowing distally, both margins stepped, anterior margin spined at 0.12 (2), 0.22 (3), 0.35 (3), 0.70 (3), 0.78 (3), and 0.89 (3), posterior margin spined at 0.19 (3), 0.36 (4), 0.62 (4), 0.82 (4), and 0.93 (4), posterodistal angle with 2 spines.

Peraeopod 5: basos broadest distally, width 0.93 length, anterior margin with large spines, posterior margin slightly scalloped with small spines; ischium posterior margin nearly straight, posterodistal angle with 2 spines; merus broadening distally, anterior margin scalloped, stepped, spined at 0.16 (1), 0.29 (2), 0.50 (3), and 0.75 (2), anterodistal angle with 4 spines, posterior margin stepped, spined at 0.22, 0.40, and 0.57, posterodistal angle with 2 spines; carpus both margins stepped and scalloped, anterior margin spined at 0.17 (2), 0.34 (3), 0.59 (2), and 0.85 (2), anterodistal angle with 3 spines, posterior margin stepped, spined at 0.35 (2), and 0.64 (2), posterodistal angle with 4 spines; propod narrowing distally, both margins slightly scalloped anterior margin spined at 0.12 (2), 0.22 (2), 0.35 (2), 0.49 (2), 0.58 (2), 0.77 (2), and 0.88 (2), anterodistal angle with 1 spine, posterior margin spined at 0.23 (2), 0.42 (2), 0.58 (2), 0.68 (3), 0.85 (2), and 0.93 (3), posterodistal angle with 3 spines.

Pleopods: all present and biramous; pleopod 1: length 0.95 mm, pleopod 2: length 0.87 mm; pleopod 3: length 0.85 mm; all have narrow peduncles with setose outer margins, inner margins have 2 coupling spines distally, rami have obscure segmentation, and have heavily setose margins; the inner ramus on each pleopod is slightly longer than the outer.

Uropod 1: peduncle with 6 dorsal spines, a large inter-ramal spur is present extending 0.41 along rami; outer ramus long, thin, somewhat wasp-waisted, naked dorsally, longer than inner, 1 long and 2 smaller terminal spines; inner ramus delicate, 4 spines on dorsal margin, 2 long and 2 short terminal spines. Uropod 2: peduncle with 4 large dorsal spines, an inter-ramal spur is present reaching 0.25 along rami; outer ramus naked, terminates with 1 long and 1 shorter spine; inner ramus heavily spined dorsally, with 2 rows of

3 spines on both the inner and the outer margins, terminates with 2 long and 2 short spines. Uropod 3: small, uniramate, peduncle with 2 dorsal spines, ramus terminates with 1 larger and 1 smaller spine. Telson: moderately cleft, each lobe has 2 marginal spines.

Female: as for male except where specified:

Length 11.2 mm, width 2.18 mm, depth 2.05 mm. Antenna 1: length 1.13 mm; flagellum of 6 podomere segments. Antenna 2: length 4.10 mm; flagellum of 17 segments. Gnathopod 1: basos anterior margin naked, posterior margin spined at 0.33, 0.53, and 0.75; propod slightly longer and narrower. Gnathopod 2: merus posterior margin with 2 more spines proximally; palm larger, palmar angle 56°, propod distal pellucid lobe slightly less produced. Broodplates: in winter stage without setae in allotype (like M.hurleyi at same season), long and narrow, with spine bases only at rounded distal ends; last pair with rolled and thickened lateral posterior margin and few spine bases distally.

Remarks

This species was abundant in the area in which it was found. It was taken with the following coastal species: Makawe hurleyi whose centre of distibution is to the north of Oamaru, and Talorchestia patersoni whose centre of distribution lies to the south. One specimen of the inland species Parorchestia ihurawao was also found at the same locality.

M.otamatuakeke is distinguished by the following combination of characters: the setose outer margins of the pleopods, the naked outer rami of uropods 1 and 2, and the double spine row on the dorsal margin of uropod 2, and the short antenna 1 which extends just to or just beyond the junction of antenna 2 peduncle segments 4 and 5. Like most New Zealand landhoppers it possesses an odd mix of advanced and primitive characters.

Genus *Tara* new genus

Diagnosis: Reticulated, semi-reticulated or spotted landhoppers with a moderately robust body, although much finer than *Transorchestia*, with pleopod peduncles naked, broodplates only setose on distal margins, and rami of uropods 1 and 2 spined on dorsal margins.

Etymology: the genus name derives from the Maori for 'spine' which is appropriate since the uropods are very spiny in this genus.

Type species: *Orchestia sylvicola* Dana, 1852. Other species: *T.sinbadensis* (Hurley, 1957); *T.simularis* (Hurley, 1957); *T.taranaki* new species; and *T.hauturu* new species.

Remarks

I have followed Bousfield's (1964) suggestion that new generic names be created for the '*sylvicola*' group, thus reserving *Parorchestia* for the *tenuis* type. The genus *Tara* contains some species with very restricted distributions. It includes coastal species, but most are true inland species found far from the sea. None seems to be widely distributed.

Tara sylvicola (Dana, 1852).

Figures 155 to 175

Orchestia sylvicola Thomson and Chilton, 1886:145; Thomson, 1881:212; Della Valle, 1893:510; Stebbing, 1899:402.

Parorchestia sylvicola Stebbing, 1899:402 (in part); Stebbing, 1906: 558; Chilton, 1911:566; Chilton, 1927:176; Stephensen, 1935:14; Shoemaker, 1935:66; Bousfield, 1964:52.

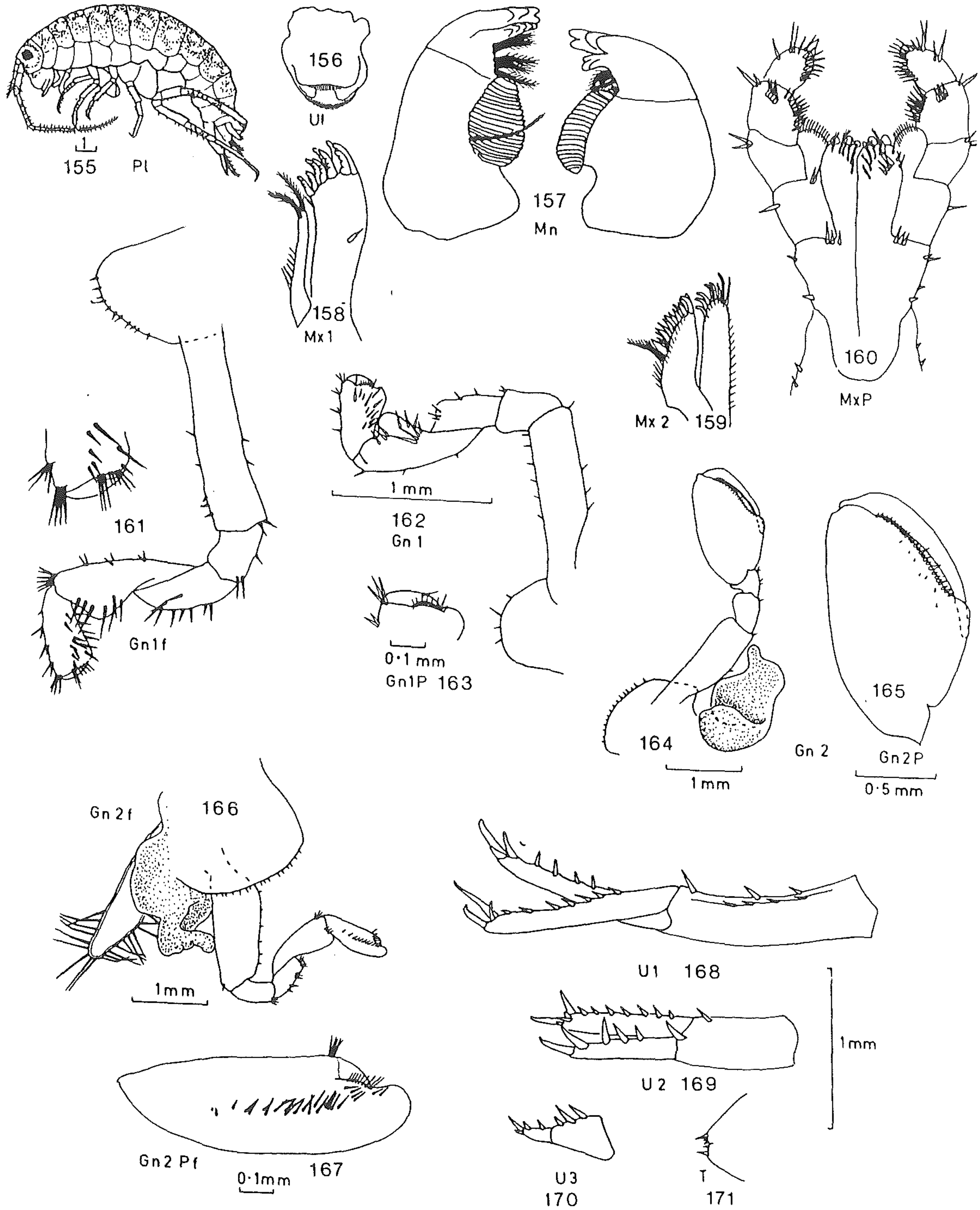
Orchestia tenuis Hurley, 1957:166.

Types:

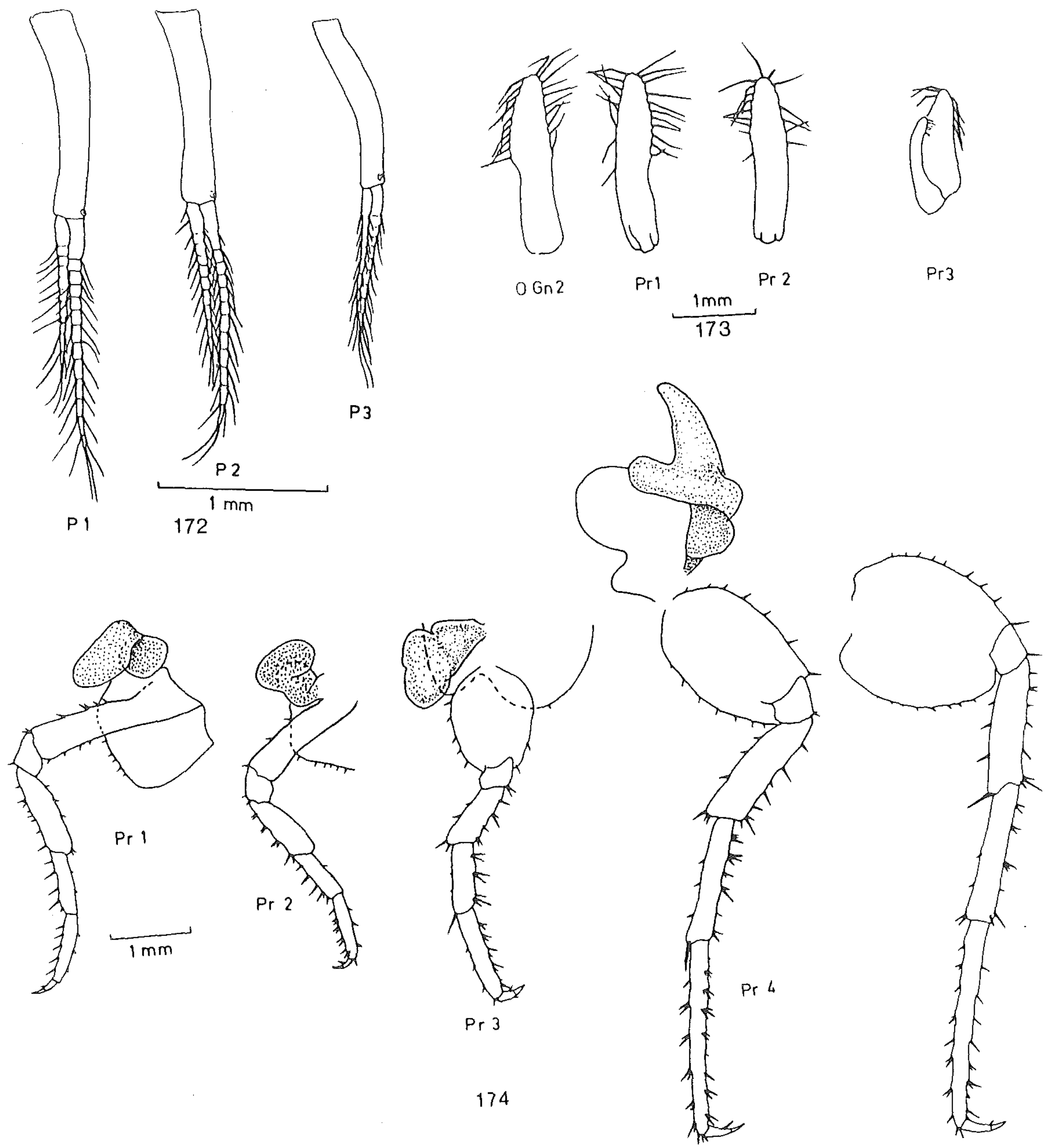
According to Hurley (1957) the holotype has been lost. Neotypes: Mt.Horokaka, Tangihua, Kaitaia, Northland, 518m, ex litter, deposited in the Canterbury Museum. Syntypes: Summit, Mangamuka Hills, Northland, deposited in the National Museum, Wellington and the Entomology Division, D.S.I.R., Auckland.

Localities and collectors:

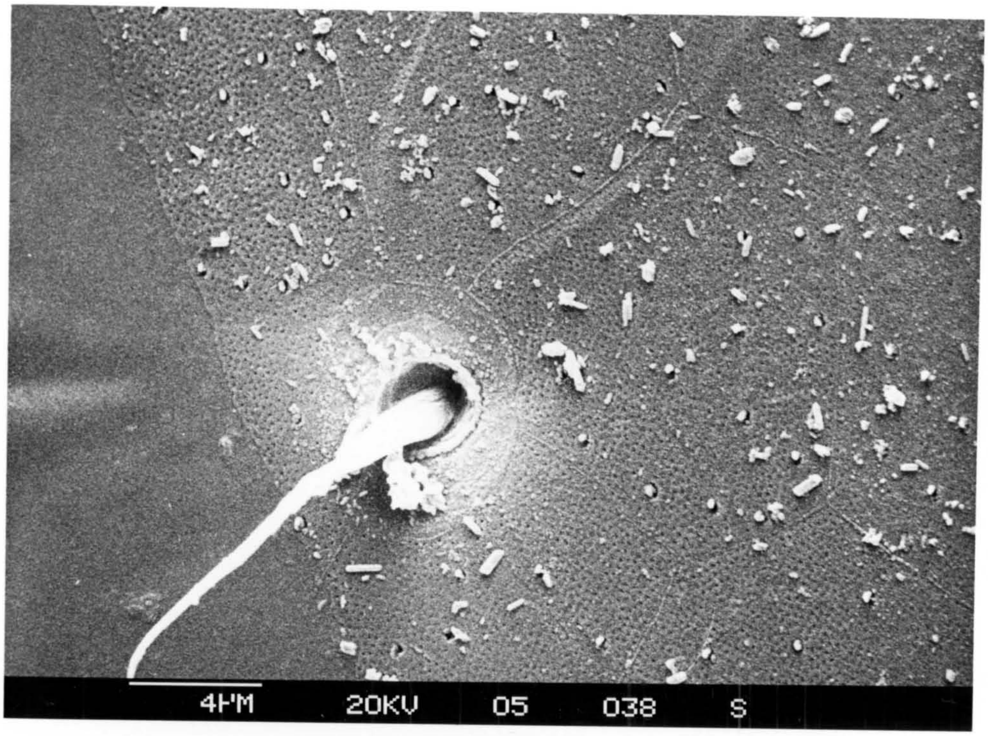
Mt.Horokaka, Tangihua, Kaitaia, 518 m, J.S.Dugdale, 16/VIII/1977, ex litter, taken with Parorchestia tenuis and Talorchestia aotearoa. Mangamuka Summit, Northland, 386 m, B.M.May, 13/XII/1976, ex litter, taken with an undescribed landhopper. Summit, Mangamuka Hills, 382 m, K.A.J.Wise, 19/XI/1966, beaten from Freycinetia and taken with P.tenuis. North side Mangamuka Hills, 300 m, K.A.J.Wise, 19/XI/1966. Forest summit, Mangamuka Hills, 382 m, K.A.J.Wise,



FIGURES 155-171. Tara sylvicola. 155, lateral aspect. 156, upper lip. 157, left and right mandibles. 158, maxilla 1. 159, maxilla 2. 160, maxilliped. 161, gnathopod 1 female. 162, gnathopod 1 male. 163, gnathopod 1 male propod. 164, gnathopod 2 male. 165, gnathopod 2 male propod. 166, gnathopod 2 female. 167, gnathopod 2 female propod. 168, uropod 1. 169, uropod 2. 170, uropod 3. 171, telson.



FIGURES 172-174. Tara sylvicola. 172, pleopods 1,2 & 3. 173, oostegites. 174, peraeopods 1,2,3,4 & 5.



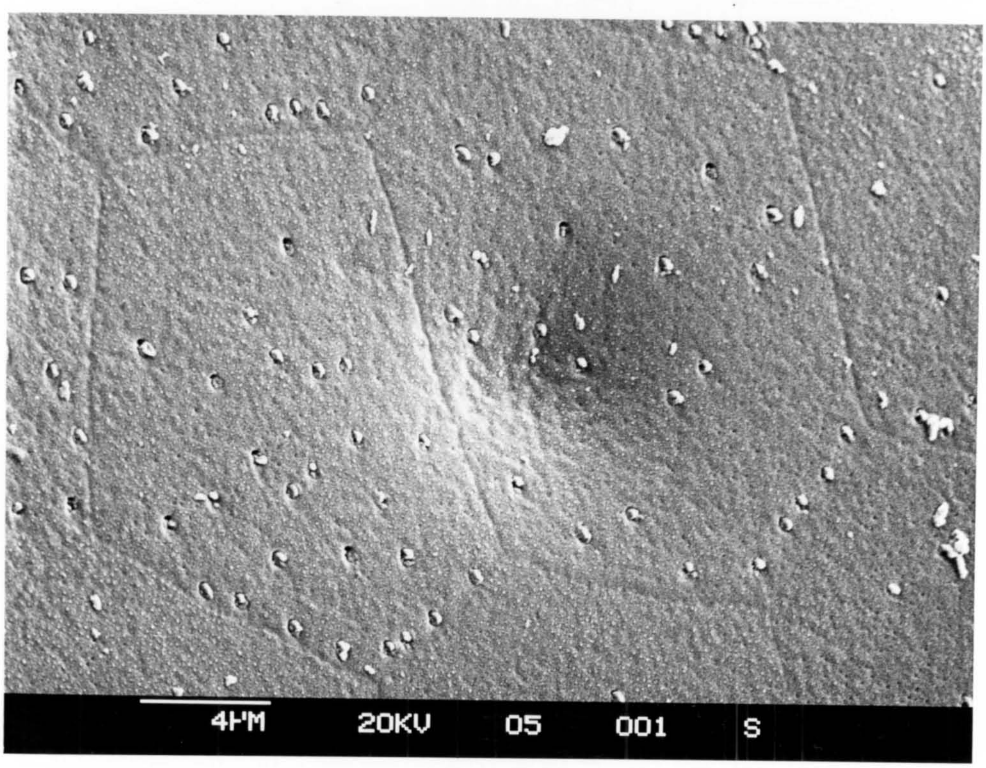


FIGURE 175. Cuticular structure of Tara sylvicola. The upper micrograph shows the dorsal surface of the second thoracic segment. A large macropore is present which opens in a dermal gland polygon. The cell boundaries are well marked. The lower micrograph shows the ventrolateral surface of the same body segment. Mesopores are scattered over the surface as well as in incomplete arcs near the two posterior margins of the cuticular polygons.

19/XI/1966. Mangamuka Gorge, K.A.J.Wise, 19/XI/1966, beaten. Three miles south of Paihia, by swamp forest, K.A.J.Wise, 18/XII/1966, ex leaf litter, taken with _T.aotearoa_. Waipu Gorge, Whangarei County, K.A.J.Wise, 20/XI/1966, ex leaf litter in forest. Tangihua Range, Tangihua Stream, J.S.Dugdale, 17/VII/1977, tributary in forest. Omahuta, J.C.Watt, 10/X/1974, in regeneration after clear-felling, near Kauri Reserve, ex litter, taken with 2 other undescribed landhopper species. Mt. Mangamuka, R.R.Forster, 7/I/1967.

Diagnosis:

A large sexually dimorphic landhopper with a reticulated body pattern, of the genus _Tara_, with large eyes, moderately long, slender antenna 2, antenna 1 reaching just beyond the beginning of the last segment of antenna 2 peduncle, gnathopod 1 strongly subchelate in both sexes, gnathopod 2 strongly chelate in male, mitten-shaped in female, peraeopods stout, pleopods slender, all present and biramous with 2 coupling spines, uropod 1 and 2 rami dorsal margins heavily spined on both branches, telson with 1 large and a few small spines on each lobe.

Description:

Male:

Length 15.9 mm, width 2.71 mm, depth 2.94 mm. Body not very deep. Pigmentation pattern reticulated. Head deeper than long. Eye round, black, about 0.33 head width. Antenna 1: length 2.10 mm, extends just beyond junction of segments 4 and 5 of antenna 2 peduncle; antenna 1 peduncle 0.79 length of flagellum; segment 1 with a small spine on dorsal margin, 1 at distal angle, and 2 on inferior margin; segment 2 as long as segment 1, with 2 spines mid-dorsally, 1 spine at superodistal angle, and laterally, and 3 longer spines at inferodistal angle; segment 3, 1.28 length segment 2, but only 0.63 its width 1 spine on superior margin, 1 spine at superodistal angle, 2 spines laterally, and 2 spines at inferodistal angle; flagellum of 8 segments, each segment except the first and last has a group of 2 to 3 spines at both the superodistal angle and the inferodistal angle; terminal tuft of about 6 short spines.

Antenna 2: length 7.55 mm; peduncle about 0.70 length flagellum; segment 3 spined on inferior margin, at inferodistal angle and around laterodistal margin, 1 spine on outer face; segment 4, 2.1 length segment 3, 4 spines on outer face, distal margin with 4 spines on outer face, 2 at inferodistal angle, and 2 on inner face, inferior margin with 5 spines; segment 5, 0.83 width segment 4, superior margin has groups of 3 spines at 0.25, 0.43, 0.64, and 0.83, inferior margin has spines at 0.14, 0.25, 0.42, 0.52, 0.63, and 0.80, inner face has spines close to inferior margin at 0.25, 0.42, 0.63, and 0.82, distal margin with 2 spines at superior, lateral and inferior angle; flagellum of 23 podomere segments, tapering distally, each podomere segment except the first and last with 3 spines at each of the 4 angles on the distal margin, terminal tuft on last segment of short setae.

Mouthparts. Upper lip: distal margin rounded, densely setulose, inner shelf naked. Left mandible with 6 cuspate incisor, lacinia mobilis 4-toothed, 8 interdentate pilose setae arranged in pairs, molar about 27-striate, molar medial seta prominent; right mandible as for left but molar medial seta not present. Lower lip of normal scroll shape, distal margin rounded, pilose, inner margin pilose, a pilose setal row runs diagonally from mid-distal margin then turns parallel with inner margin. Maxilla 1 inner plate slender and narrowing distally, inner margin finely pilose, terminating with 2 long pilose setae, outer plate broadening distally, distal margin with 9 teeth having 1, 1, 4, 4, 4, 4, 4, 4, 4, lateral teeth (from outer to inner). Maxilla 2 outer plate margins subparallel, distal margin rounded with about 20 setae curved inwards, inner margin sparsely pilose, outer plate narrowing distally to a point, from the apex to mid-distal the inner margin is fringed with setae, this row terminates in a stout pilose seta, the inner margin is sparsely pilose proximally. Maxilliped inner plate distal margin rounded with 3 stout spine teeth, pilose setae are set below these and down inner margins; outer plate with a spine comb row distally and down inner margins, inner margin with a patch of about 4 spines midway; basal segments with spines at outer distal angles and a patch of 3 spines on mid-distal margin; palps broad, segment 1 with 3 spines on outer distal angle and a patch of 4 spines on inner distal angle, segment 2 outer distal angle with 3 spines, inner distal angle with 4 spines, inner margin produced inwardly and with a fringing setal comb of 10 or more seta on both sides; segment 3 heavily spined on inner margin and distally; segment 4 present and not obscured by segment 3 spines.

Gnathopod 1: coxal plate ventral margin rounded, with 4 spines; basos broadening immediately proximally then subparallel for the distal 2/3 of its length, anterior margin straight, spined at 0.44, 0.55, 0.66, 0.77, 0.86, and 0.95, posterior margin angled initially, with stouter spines at 0.37, 0.49, and 0.62 and at distal angle; ischium a rhomboid with 2 spines at posterodistal angle; merus not much longer than ischium, posterior margin with about 6 spines and produced distally into a pellucid lobe; carpus anterior margin somewhat convex, spined at 0.24, 0.42, and 0.66, 2 large spines at anterodistal angle, posterior margin produced into a large pellucid lobe, guarded at its base by a row of 4 stout spines on both the inner and outer faces, posterodistal angle with 5 stout spines; propod broadening distally, produced a little posterodistally into a pellucid lobe which projects apically beyond the dactyl tip, anterior margin spined at 0.38 (1), 0.63 (2), and 0.83 (3), anteriodistal angle with 4 spines, inner face has a longitudinal row of 11 stout spines starting from near proximal posterior margin to the anterior of the palm, outer face has 2 longitudinal rows, one of 4 and the other of 5 stout spines, palm transverse, convex, about 0.5 propod width, fringed with a row of about 12 spines on each side, dactyl about 0.75 width.

Gnathopod 2: coxal plate rounded ventrally with 15 spines; gill trilobed but distal lobe short and narrow; basos broadening distally, anterior margin very slightly sinuous, naked, posterior margin convexly rounded, with small spines at 0.35, 0.49, 0.58, and 0.67, posterodistal angle with 2 small spines; ischium produced anteriorly into a prominent pellucid lobe, posterodistal angle with 2 small spines; merus; shorter than ischium, posterior margin with 2 spines, posterodistal angle with 2 spines; carpus short, with 1 spine on anterior margin; propod greatly expanded broadening distally, triangular, anterior margin convexly curved, posterior margin short, straight, palm slightly convex, fringed on both sides by numerous short setae with those on the outer face being the shortest, there are about 30 spines in each row, and the spines increase in size posteriorly, palmar angle 143^{o}, palm terminates in a transverse lobe which guides and protects the dactyl tip; dactyl long, curved, inner margin with a few needle setae, distal end with rounded inflexible tip, overlaps propod.

Peraeopod 1: coxal plate ventral margin slightly rounded convexly, spined; gill discoidal, smaller than that of gnathopod 2 but almost reaches midline; basos long, subparallel, curved somewhat anteriorly, anterior margin concave, with small spines at 0.43, 0.57, 0.68, 0.72, and 0.81, posterior margin with larger spines at 0.25, 0.32, 0.45 (2), 0.66, posterodistal angle with 2 spines; ischium anterior margin slightly produced to a pellucid lobe, posterodistal angle with 3 spines; merus broadening distally, anterior margin spined at 0.17 (1), 0.33 (1+1), and 0.55 (1+1), anterodistal angle with 2 spines, posterior margin sinuous, spined at 0.24 (3), 0.40 (3), 0.54 (1), 0.60 (1), 0.66 (1), 0.79 (1), and 0.96 (1), posterodistal angle with 1 spine; carpus anterior margin spined at 0.31 (1), and 0.59 (2), anterodistal angle with 3 spines, posterior margin spined at 0.19 (1+1), 0.39 (1+1), 0.63 (1+1), 0.81 (2), and 0.86 (1), posterodistal angle with 1 spine; propod curved slightly posteriorly, anterior margin spined at 0.27 (2), 0.50 (2), and 0.79 (2), anterodistal angle with 1 spine, posterior margin curved slightly convexly, spined at 0.14 (1), 0.23 (2), 0.35 (3), 0.53 (3), 0.69 (3), and 0.88 (5); dactyl comparatively long with 1 spine on inner margin. Peraeopod 2: coxal plate subsquare, ventral margin nearly straight with 9 spines, posterodistal angle rounded; gill ovately discoidal; basos anterior margin concave, with small spines at 0.72, 0.80, and 0.86, anterodistal angle with 2 spines, posterior margin spined at 0.28 (1), 0.38 (2), and 0.63 (1), posterodistal angle with 3 spines; ischium anterior margin slightly produced to a lobe, posterodistal angle with 2 spines; merus broadening distally, anterior margin with spines at 0.22 and 0.44, anterodistal angle with 3 spines, posterior margin with larger spines at 0.25 (1+1), 0.46 (3), and 0.70 (3), posterodistal angle with 3 stout spines; carpus anterior margin with small spines at 0.31 (1), and 0.58 (2), anterodistal margin with 3 spines, posterior margin with larger spines at 0.19 (1+1), 0.38 (1+1), 0.64 (1+2), 0.74 (1), 0.81 (2), and 0.90 (1); propod margins subparallel only slightly curved posteriorly, anterior margin spined at 0.25 (2), 0.46 (2), and 0.73 (3), anterodistal angle with 4 spines, posterior margin with spines at 0.19 (1), 0.30 (3), 0.46 (3), 0.63 (3), 0.68 (1), 0.82 (3), and 0.87 (1). Peraeopod 3: coxal plate both ventral lobes rounded and spined; gill comparatively large with 2 slightly developed lobes; basos an inverted pear shape, width 3/4 length, anterior margin spined at 0.25 (2), 0.41 (1), 0.55 (1), 0.66 (1), and 0.76 (2), anterodistal angle with 3 spines, posterior margin spined at 0.06, 0.19, 0.35, 0.68, 0.81, and 0.94; ischium short, spined at anterodistal angle, posterior margin slightly produced; merus broadening distally, anterior margin spined at 0.24 (3), 0.51 (3), and 0.76 (3), anterodistal angle with 5 spines, posterior margin spined at 0.32, and 0.56, posterodistal angle with 4 spines;

propod narrowing slightly distally, 7 times longer than broad, anterior margin spined at 0.20 (2), 0.32 (2), 0.46 (3), 0.65 (4), and 0.85 (3), posterior margin spined at 0.37 (1), 0.59 (4), and 0.85 (3), posterodistal angle with 5 spines. Peraeopod 4: coxal plate ventral margin rounded with few small spines; gill large, multilobed, pendulate lobe large, somewhat triangular; basos ovate, width 0.80 length, anterior margin spined at 0.07, 0.18, 0.26, 0.40 (2), 0.54 (2), 0.70 (1), 0.81 (2), and 0.89 (1), anterodistal angle with 2 spines, posterior margin spined at 0.31, 0.40, 0.46, 0.51, 0.58, 0.69, 0.78, 0.86, and 0.92; ischium with 2 spines at anterodistal angle; merus slightly broadening distally, anterior margin spined at 0.12 (1), 0.24 (2), 0.33(1), 0.46 (3), 0.58 (1), 0.70 (3), and 0.81 (1), anterodistal angle with 4 spines, posterior margin spined at 0.14 (1), 0.24 (1), 0.39 (1), and 0.63 (1+1), posterodistal angle with 3 spines; carpus subparallel, anterior margin spined at 0.15 (2), 0.30 (2), 0.44 (1), 0.57 (4), 0.77 (2), and 0.91 (3), posterior margin with smaller spines at 0.36 (2), 0.53 (2), and 0.77 (1), posterodistal angle with 2 large spines; propod width 0.10 length, anterior margin spined at 0.14 (2), 0.24 (3), 0.36 (2+2), 0.49 (2+2), 0.56 (2+2), 0.71 (2), 0.82 (3), and 0.94 (2+2), posterior margin spined at 0.23 (2), 0.34 (3), 0.51 (3), 0.61 (1), 0.68 (3), 0.85 (3), and 0.95 (3), posterodistal angle with 4 spines; dactyl coniform, slightly curved anteriorly. Peraeopod 5: coxal plate ventral margin rounded, spined; penal organ subsquare; basos ovate, as wide as long, ischium with 3 spines at anterodistal angle, posterior margin only slightly produced; merus broadening only slightly distally, anterior margin spined at 0.12 (2), 0.25

(3), 0.36 (2), 0.49 (2+2), and 0.74 (2+1), anterodistal angle with 4 spines, posterior margin spined at 0.11 (1), 0.21 (1), 0.41 (1+1), and 0.67 (1+1), posterodistal angle with 1+2 spines; carpus margins subparallel, width 0.18 length, anterior margin spined at 0.15 (2), 0.29 (2), 0.43 (0+2), 0.55 (2+2), 0.75 (2), and 0.89 (3), posterior margin with smaller spines at 0.25 (2), 0.35 (2), 0.52 (2), and 0.74 (2), posterodistal angle with 4 spines; propod narrowing slightly distally, curved slightly anteriorly, width 0.09 length, anterior margin spined at 0.16 (1), 0.25 (2), 0.37 (3), 0.49 (3), 0.59 (3), 0.70 (2), 0.79 (3), 0.86 (1+1), and 0.91 (2+1), posterior margin spined at 0.15 (2), 0.22 (3), 0.35 (3), 0.48 (3), 0.59 (3), 0.69 (3), 0.83 (3), and 0.96 (3), posterodistal angle with 2 spines.

Pleopods all present, slender, and biramous; all with 2 coupling spines, outer ramus on each is the smaller, margins of peduncle naked, rami segmented; lengths: first, 2.85 mm, second 2.69 mm, third 2.15 mm.

Epimeral plate 1: subtriangular, posterodistal angle with only a small 'hook', posterior margin with 2 small spines; Epimeral plates 2 and 3: subsquare but with rounded anterodistal angles, moderate 'hooks' on posterodistal angles, posterior margins with 5 small spines.

Uropod 1: moderately long, peduncle with about 8 spines in each of 2 rows dorsally, inter-ramal spur minute, both rami heavily spined dorsally, and both terminate with 2 large and 2 smaller spines. Uropod 2: peduncle spined dorsally, short, stout inter-ramal spur present, both rami spined dorsally, the outer ramus has 3 very large spines while the inner has 7 smaller spines.

Telson: bilobed but only slightly cleft, with a cluster of about six spines around the apex of each lobe, but only one of these spines is large.

Female: - as for male except where noted:

Length 18.8 mm, width 3.41 mm, depth 3.65 mm. Antenna 1: length 2.42, extends to about 1/5 along antenna 2 peduncle segment 5; segment 2 with 3 spines mid-dorsally, segment 3 with 2 spines on superior margin, with 1 spine on inferior margin; flagellum with 8 segments. Antenna 2: length 9.43 mm, peduncle length about 0.65 flagellum length; flagellum with 24 podomere segments.

Mouthparts. Mandibles: molar medial setae not discernable.

Gnathopod 1: sideplate anterodistal angle sharper than in male; posterior margin with an additional spine at 0.81; ischium with a prominent spine on posterior margin; merus not produced into pellucid lobe; propod narrower than in male, width only 0.45 length, palm extends to edge of propod, fringed by larger spines than in male; dactyl almost propod width.

Gnathopod 2: brood plate narrowing distally, end rounded, with about 21 spines; basos broader proximally, narrower distally, broader than male, 0.34 length, posterior margin with spines at 0.35, 0.49, 0.59, 0.69, 0.76, 0.86, and 0.94; merus with 3 marginal spines, 4 spines on lateral face, and 2 at posterodistal angle; carpus long, broadening distally with a pellucid lobe posterodistally, 3 spines at anteriodistal angle, 2 spines at posterodistal angle, about 7 spines on lateral face; propod mitten-shaped, long, broadening distally into a pellucid lobe posterodistally which projects beyond the palm, weakly subchelate, palm only about 0.33 propod width, palmar angle 18°; dactyl short, tip occludes into propod lobe.

Peraeopod 1: broodplate margins subparallel, rounded distally, with about 20 spines; basos broader, anterior margin straighter than in male; merus anterior margin spined at 0.17, 0.33, 0.55, and 0.70. Peraeopod 2: broodplate narrowing somewhat distally; merus slightly broader. Peraeopod 3: broodplate somewhat cup-shaped with posterior margin upturned and folded forwards, distal margin tapering into a spined lobe with about 9 spines; peraeopods 3, 4 and 5 more massive than male, but shape and spination basically the same.

Uropod 1: peduncle dorsal margin with 2 rows of spines, terminating distally with a large spine, inter-ramal spur absent; both rami spine dorsally with 9 spines each; the spines become larger distally, all spines are scionate, 2 large scionate spines and 2 smaller spines terminate each ramus. Uropod 2: peduncle dorsal spines small except for 4 in 2 groups on the distal margin, inter-ramal spur short and stout; outer ramus with 4 stout spines on dorsal margin; inner ramus with 2 rows of dorsal spines running longitudinally, one row with 11 spines, the other with 3, terminal spines on both rami consist of 2 large and 2 small. Uropod 3: uniramate; peduncle with 5 stout spines dorsally; ramus with 2 spines on mid-dorsal margin and 1 on mid-ventral margin; terminal spine cluster consists of 1 large and 3 smaller spines.

Remarks

In 1852 Dana described the female *Orchestia sylvicola* from moist soil in the bottom of the extinct volcano of Taiamai - now called Ohaeawai - in the Bay of Islands, as a species with spined outer rami of uropod 1 and many other characters sufficient to clearly delineate it from other landhopper species. He amplified his description in 1853 and 1855. Unfortunately, he was not able to associate a male with the female with certainty. He described a male which had been collected from either the Bay of Islands or the volcano Taiamai as *Orchestia sylvicola*, but mentioned that the difference in uropod spination (the male had a naked outer ramus) suggested that the male and female did not belong to the same species. It was his opinion that if they did not belong together then the male was in fact *O.tenuis*, a species that he described from the same general area. *Parorchestia tenuis* is very similar in gross morphology, but beside the specific point mentioned by Dana of the difference in uropod spination, there were other differences given in his drawings and text which clearly differentiated the two species. These include: the length of antenna 1 in relation to the peduncle of antenna 2 (that of *P.tenuis* is much longer), the general shape of the body, especially depth (*P.tenuis* is shallower), the length and conformation of the peraeopods (*T.sylvicola* has longer peraeopods), the robustness of the uropods, and the shape of the gnathopods. Unfortunately, Dana's types have been lost and confusion has reigned over the two species for a very long period.

Spence Bate (1862) repeated Dana's descriptions of the female and reproduced his figures. He also described a male of T.sylvicola collected by the Erebus and Terror Expedition from New Zealand which appears from the figures to have a spined outer ramus, but his description was not sufficient to clarify the matter.

Thomson (1881) suggested a radical solution: to unite T.sylvicola, P.tenuis and the supralittoral O.novae-zealandiae in Orchestia sylvicola. He postulated that this species is polymorphic, having more than one adult form. This conclusion was based on collections he made from ferns etc on Otago Peninsula, from cocksfoot and other grasses in the Town Belt, Dunedin, from bush on Flagstaff, Dunedin district, from Preservation Inlet, from bush at Port Pegasus, Stewart Island, from Copper Island, Stewart Island, and from bush in the neighbourhood of Dunedin. From the examination of the 163 specimens that he collected he concluded that they all belong to one variable species. He stated (p.212): "The antennae vary greatly in length; thus the superior pair in some extend only as far as the extremity of the penultimate joint of the lower, while in others they extend as far as the extremity of the ultimate. In some cases the inferior pair are not one-third as long as the animal; in others they are more than half as long. Some exhibit a regular gradation in length of the 3rd, 4th, and 5th peraeopoda; others have the 3rd and 4th subequal and short, and the 5th very long ...."

It is obvious that he was examining a mixed species collection, probably consisting of Makawe hurleyi, Talorchestia patersoni (the latter species would provide the few males with large second gnathopods in his collection), and Parorchestia ihurawao; all of which are common in the Dunedin district, while from his Stewart Island sites he would have taken T.patersoni, Kanikania motuensis plus some of the other species that occur on Stewart Island such as Parorchestia tenuis. None of his material would have included sylvicola as Dana described it. It is surprising that he did not detect that he had a multiplicity of species since he collected the material himself, and the pigmentation colours and patterns of these species around Dunedin and Stewart Island are species specific and very distinctive. He did note the multiplicity of colours in his sample, but seemed unaware of the implications of this observation. He makes no mention of the far more important pattern characteristics by which species can be readily identified. It is a great pity that he did not examine material from the type locality designated by Dana. Systematic conventions require this, if at all possible, before taking such a radical step as merging three species which were, by the standards of the day, well described.

The confusion reigning in both the ecological and the taxonomic literature since Thomson's time has been considerable. Stebbing (1906) redescribed both species giving more detail apparently from new material. What material it was we have no knowledge, but unfortunately his description of P.sylvicola is internally inconsistent and is not consistent with Dana's description. For instance, he states that:

"Antenna 1 reaching end of penultimate joint of peduncle of antenna 2, but sometimes much farther."

This seems a simple case of species confusion; the sympatric species Talorchestia aotearoa has longer antennae and it looks like the female of P.sylvicola. It is commonly collected together with Tara sylvicola and P.tenuis in Northland. Later he states:

"Uropods 1 and 2, outer ramus with spines only at apex, in both sexes (Dana: only in male)."

This description of T.sylvicola does not agree with that of Dana who established the species.

Chilton (1925) recorded Parorchestia sylvicola (Dana) from Wharekauri in the Chatham Islands and stated that this is the common terrestrial amphipod of New Zealand. He gave as its distribution: New Zealand, Chatham Islands, Kermadec Islands, Lord Howe Island. The species he collected from the Chathams was probably Makawe hurleyi which is the commonest landhopper on the islands, it also occurs on the east coast of the South Island. I have never seen any collections containing Tara sylvicola from the Chatham Islands and I have been unable to locate Chilton's original Chatham Island material.

Stephensen (1938) lists sylvicola as having no spines on the outer ramus, but mentions that some specimens from New Zealand, as determined by Stebbing, in the Zoological Museum of Copenhagen, have about 4 marginal spines.

In his 1957 review of the genus Orchestia, Hurley discussed the question of the validity of T.sylvicola at length. He considered that it was not practical to separate tenuis and sylvicola on the basis of written descriptions so he proposed to merge them under tenuis, in the genus Orchestia, along with Orchestia gammarellus Della Vale, Allorchestia recens Thomson, and two forms of P.stewarti Stephensen. He was correct in saying that the written descriptions are confusing; they certainly have been so since Dana's original descriptions. But since the two species can be distinguished using Dana's descriptions, it is invalid to merge them.

There is no evidence of anyone, with the possible exception of Spence Bate, examining new material from Northland probably since Dana's time. If they had, the confusion would have been resolved easily. The material I have examined shows that P.tenuis and T.sylvicola co-exist in Northland. P.tenuis extends beyond Northland to the rest of the North Island, especially in upland areas of low soil conductivity, and to Nelson and Westland in the South Island, to Stewart Island, and perhaps Snares Island. T.sylvicola, on the other hand, is restricted to Northland. Dana's attribution of the male to T.sylvicola was, as he suspected, incorrect; it belongs with P.tenuis. Both sexes of T.sylvicola have spined outer rami on uropod 1.

This species is easily identified by its reticulated body pattern, the shortness of the antenna 1 relative to antenna 2 peduncle, and the very distinctive male second gnathopod propod and dactyl. It seems to persist in spite of environmental disturbance since it has been taken in cut-over forest areas which are now regenerating. Evidently, it has not penetrated non-native communities as have other similar landhoppers such as *P.tenuis* and *M.hurleyi*. This is probably because the aggressive and ubiquitous *Talitroides topitotum*, an adventive landhopper from India, is widespread throughout the Auckland urban area and Northland where it generally occupies both the long grass and the disturbed scrubland habitats, displacing the native species from such areas.

<u>Tara taranaki</u> new species

Figures 176 to 200

Types:

The holotype male was collected from Dawson Falls, Mt Egmont, at 945 m, by G.W.Ramsay, 14/X/1955, and has been deposited in the Canterbury Museum. The allotype female was collected from Holly Hut, 950 m, Taranaki, by K.J.Fox, -/XI/1975, and has been deposited in Canterbury Museum . Author's catalogue no. KD 686 and KD 854. Paratypes have been deposited in the National Museum, Wellington.

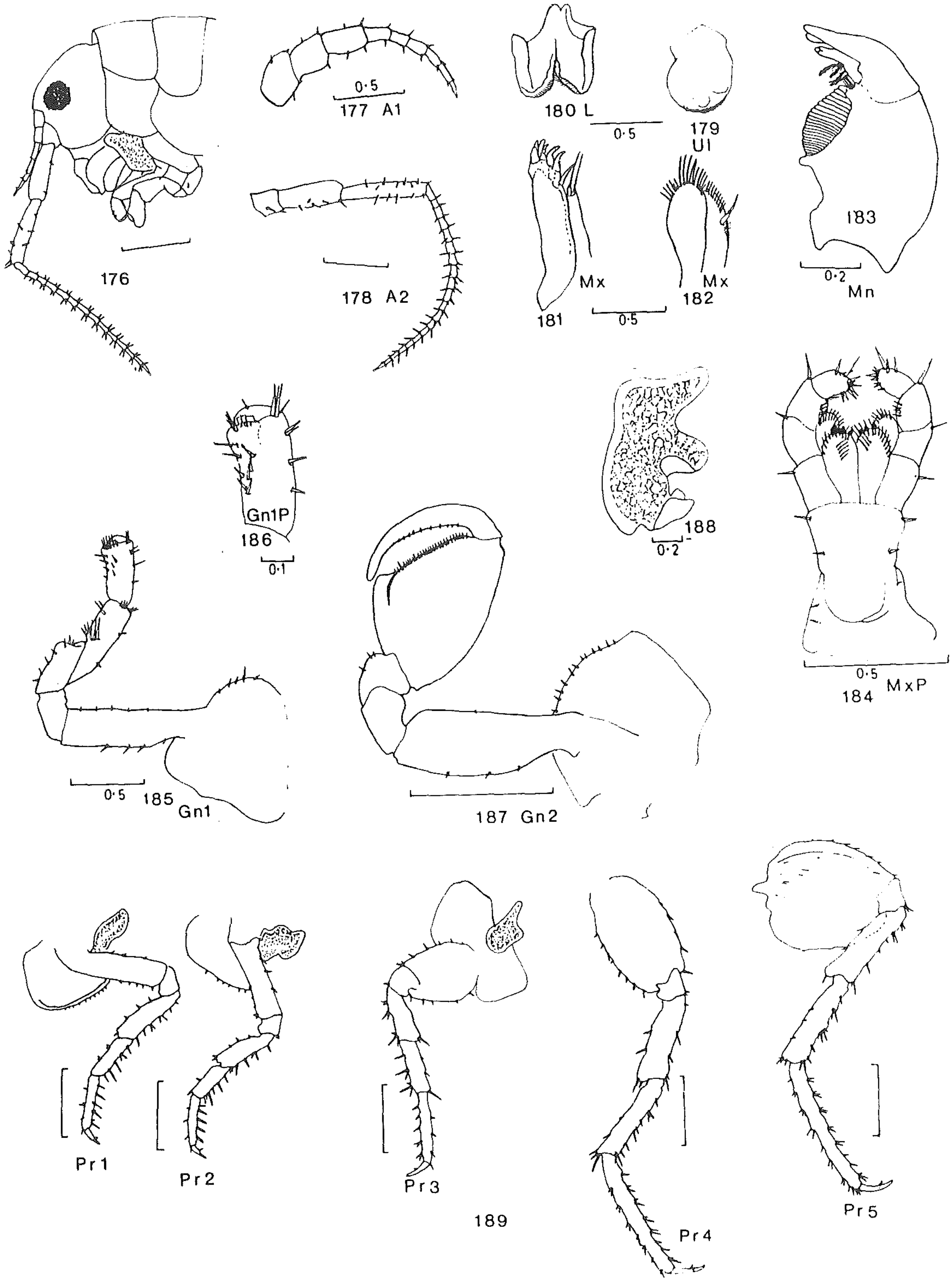
Localities and collectors:

Holly Hut, 950 m, Mt Egmont, coll. A.K.Walker, 26/XI/1975, 1 female collected at night. Dawson Falls, Mt Egmont, 945 m, coll. G.W.Ramsay, 14/X/1955, 1 male (holotype) and 1 mature female. Holly Hut, Mt Egmont, 950 m, coll. K.J.Fox, 26/XI/1975, 1 large female with a brood of 12 eggs taken by beating <u>Cordyline indivisa</u> (allotype female).

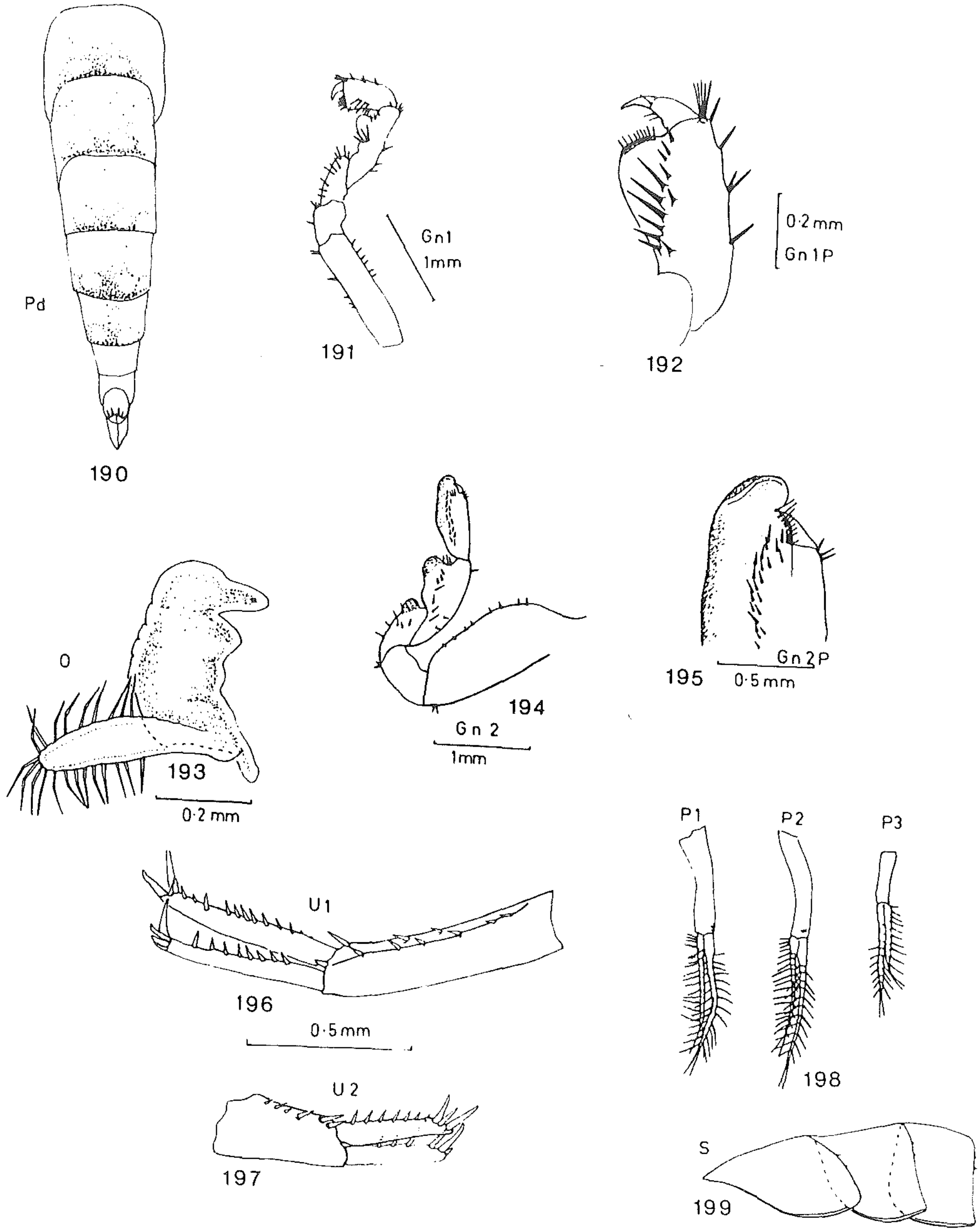
Etymology: the specific epithet is derived from the type locality, Taranaki, the Maori name for Mt Egmont.

Diagnosis:

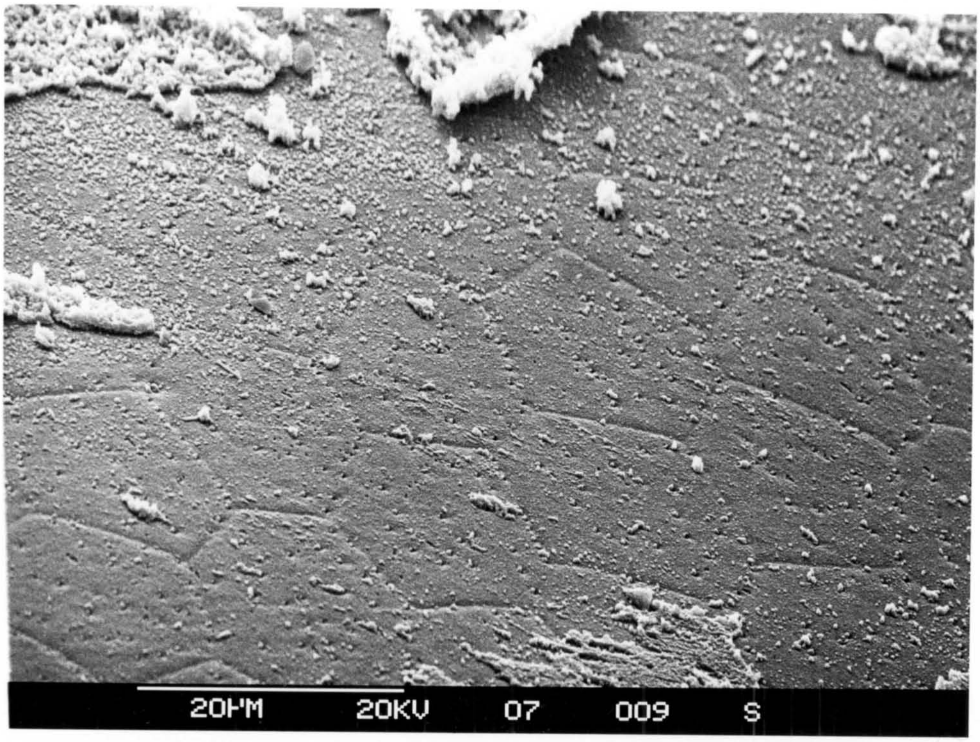
A large, strongly sexually dimorphic landhopper, of the genus <u>Tara</u>, eyes large; antenna 2, moderately long, slender; antenna 1 extends just beyond the beginning of the last segment of antenna 2 peduncle: gnathopod 1 strongly subchelate in both sexes, gnathopod 2 strongly



FIGURES 176-189. Tara taranaki male. 176, cephalon. 177, antenna 1. 178, antenna 2. 179, upper lip. 180, lower lip. 181, maxilla 1. 182, maxilla 2. 183, mandible. 184, maxilliped. 185, gnathopod 1. 186, gnathopod 1 propod. 187, gnathopod 2. 188, gnathopod 1 gill. 189, peraeopods 1,2,3,4 & 5.



FIGURES 190-199. Tara taranaki female. 190, dorsal aspect. 191, gnathopd 1. 192, gnathopd 1 propod. 193, gnathopod 2 gill and oostegite. 194, gnathopod 2. 195, gnathopod 2 propod. 196, uropod 1. 197, uropod 2. 198, pleopods 1,2 & 3. 199, epimeral plates.



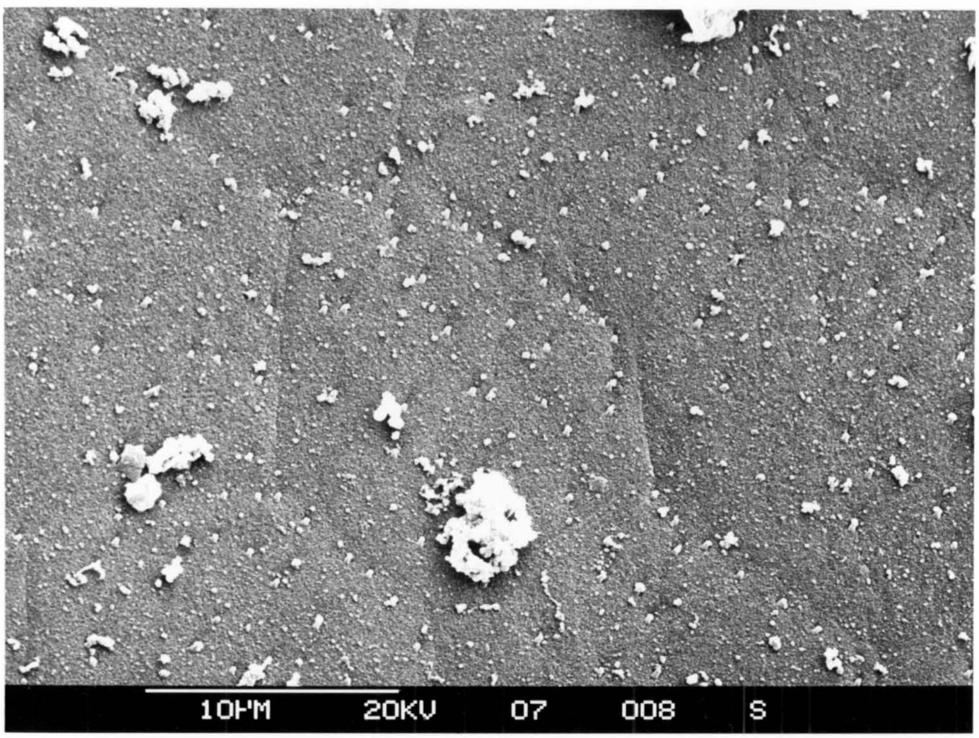


FIGURE 200. Cuticular structure of Tara taranaki. The upper micrograph shows the midlateral surface of thoracic segment 2. The cuticular polygons are well defined, mesopores are scattered over the surface as well as being arranged in arcs near the two posterior margins of the polygons. The lower micrograph shows a more ventral view of the same body segment. The mesopores show plugs of mucoid material. Larger aggregations and sheets of mucoid material are present in both micrographs.

chelate in male, mitten-shaped in female, in both sexes the basos of this appendage is broadened, peraeopod stout, pleopods slender but all present and biramous with only 2 coupling spines, uropod 1, and 2 rami dorsal margins heavily spined on both branches.

Description:

Male:

Length 14.9 mm, width 2.8 mm, depth 2.5 mm. Body not very deep. Pigmentation pattern unknown. Head deeper than long. Eye round, black, about 0.33 head length. Antenna 1 length 1.7 mm, extends to just beyond junction of segments 4 and 5 of antenna 2 peduncle; peduncle segment 1 spined at 0.66 on both margins and at distal angles; segment 2 spined at 0.5 on upper margin and at distal angles; segment 3 longer than 1 and 2, spined at 0.5 on both margins and at distal angles; flagellum about as long as peduncle with 6 podomere segments, each podomere spined at distal angles, terminal tuft short and close bound. Antenna 2: length 6.4 mm, peduncle about 0.75 length flagellum, peduncle segment 1 with a spine at inferodistal margin, peduncle segment 2 with a row of single spines inferiorly and a single spine a little superior to the spine midway on the inferior margin, a larger spine is present on the inferodistal margin; peduncle segment 3 is the longest, with spines in axial rows of up to 4 spines per row; flagellum slender with each of the 20 podomeres not greatly expanded distally, spines in four groups on distal margins of each podomere, each spine group may consist of 1, 2 or 3 spines, the lower numbers may result from wear or breakage; ultimate podomere is longer than penultimate and has a terminal tuft of spines which is very short (less than 0.2 podomere length).

Mouthparts: upper lip normal with setose margin ventrally. Mandible with 8-cuspate incisor, lacinia mobilis 4-toothed, inter-dentate pilose setae evenly spaced, molar setal tuft present but short, molar 32-striate. Lower lip scroll-shaped deeply cleft, heavily sclerotised on inner margins, setae on inner margins more robust than those more distal on the same margins. Maxilla 1, inner plate slender, narrowing distally, with two terminal setae heavily pilose; outer plate broad, distal margin with 9 teeth having 2, 1, 3, 3, 3, 3, 3, 3, 1 lateral teeth (from outer to inner). Maxilla 2 plates broadening distally; inner plate, inner margin setose proximally, a stout pilose seta terminates a row of inwardly curved spines on distal margin; outer plate with row of inwardly curved spines distally. Maxilliped narrower than normal, with inner plates broadening distally, distal margin with 3 teeth of which the inner is the smaller and the other two are subequal, pilose setae are set in between the teeth, the outer distal margin lateral to the teeth is fringed by a double rowed spine comb; outer plate distally rounded, with a row of pilose setae set back from the distal margin and projecting beyond it; palp segment 1 with a single spine at outer distal margin, segment 2 with a double spine on outer margin, inner margin scarcely produced inwards, with a comparatively sparse spine comb fringing the inner margin, segment 3 only sparsely spined, segment 4 not distinct, but not masked by segment 3 spines.

Gnathopod 1: coxal plate ventrally rounded with 6 spines; basos anterior margin nearly straight, with 3 small spines equally spaced at 0.5, 0.65, and 0.8, spined at distal angle; posterior margin parallel distally, with stouter spines at 0.35, 0.5, and 0.7, spined distally; ischium narrower than basos, spined on posterodistal angle; merus with the usual extremely short anterior margin, posterior margin with projecting pellucid lobe at about 0.75 on outer margin (this possibly protects the tip of the reflexed propod), proximally to the lobe posterior margin with 3 equally spaced stout spines, while around the lobe base are 3 spines, distally from the lobe is a patch of short setae; carpus anterior margin convex, with two small single spines, marginally and a patch of 3 stouter spines at distal angle, inner face with 4 long spines, posterior margins each with two long spines; propod subrectangular but with posterior margin slightly produced distally into a small scabrous lobe; anterior margin with 3 spine groups, anterodistal angle with 4 long spines, posterior margin with about 4 longer spines, chelate, with palm 0.6 propod width fringed with 2 rows of 6 spines each; finger shorter than palm.

Gnathopod 2: coxal plate rounded ventrally with 20 spines equidistant along margin; gill large and trilobed; basos narrowest proximally, broadest medially, anterior margin sinuous proximally but straight for most of its length, spineless, posterior margin broadening medially but narrowing distally, with 3 spines equidistant; ischium has 2 strongly convex spineless anterior margins with an axial groove between them to receive the reflexed merus-carpus, posterior margin naked, posterior distal angle spined; merus posterior margin with 3 spines; carpus short, spineless; propod greatly produced, subtriangular, broadening distally, margins naked, anterodistal angle with 2 small spines, palm only slightly convex, fringed by rows of many short but stout spines, palm terminates in raised sclerotic area onto which the dactyl tip occludes, palmar angle 145°; dactyl strongly recurved, longer than propod is broad, with about 12 small cylindrical (i.e. non-conical) spines set a little retrogradely. Peraeopod 1: coxal plate ventral margin slightly convex, spined; gill simple, moderately large; basos broadening a little distally, anterior margin slightly recurved concavely, with 3 small spines, anterodistal margin spined, posterior margin with stouter spines at 0.20 (1), 0.25 (2), 0.44 (2), 0.69 (2), posterodistal angle spined; ischium subrectangular, spined at posterodistal angle; merus broadening distally, anterior margin recurved slightly convexly, with spines at 0.20 (1), 0.36 (1), and 0.57 (1), anterodistal angle with 3 spines, posterior margin slightly sinuous with spines at 0.15 (2), 0.27 (3), 0.44 (2), 0.64 (3), 0.80 (2), 0.93 (3), posterodistal angle spined; carpus shorter and narrower than merus, broadening only slightly distally, anterior margin with spines at 0.38 (2), and 0.65 (2), anterodistal angle with 2 smaller spines, posterior margin with stout spines at 0.20 (1+2), 0.40 (2+1), 0.63 (1+1), 0.82 (2), 0.86 (0+1), and 0.92 (1); propod narrower but longer than carpus, posterior margin with spines at 0.16 (0+1), 0.30 (1), 0.55 (1), 0.80 (1), anterodistal angle with 1 spine, posterior margin with spines at 0.22 (1), 0.35 (1+1), 0.52 (1+1), 0.71 (1+2), 0.85 (1+1), and 0.92 (1).

Peraeopod 2: coxal plate ventral margin straight and spined, rounded posteriorly, posterior margin spined; basos subrectangular, anterior margin only slightly concave, with 2 spines at 0.70, 0.80, and 0.90, anterodistal angle with 2 spines, posterior margin almost straight with stout spines at 0.25 (1), 0.43 (1+2), and 0.66 (1+2), 1 spine at posterodistal angle; ischium with 2 spines at posterodistal angle; merus broadens distally, anterior margin with 3 stout spines, anterodistal angle with 4 spines, posterior margin with 3 groups of 2-3 stout spines, posterodistal angle with 3 large spines; carpus slightly shorter than that of peraeopod, broadening a little posterodistally, anterior margin with 1 group of 2 small spines at 0.60, anterodistal angle with 3 spines, posterior margin with stout spines; propod anterior margin with 3 groups of stout spines, anterodistal angle spined, posterior margin with 5 groups of spines (1 large, 2 smaller).

Peraeopod 3: coxal plate rounded ventrally with ventral margin having 5 spines; gill somewhat discoidal; basos produced into an elongated ellipsoid with the anterior margin less convex than posterior, stout spines on the anterior margin at 0.16 (1), 0.29 (1), 0.43 (2), 0.63 (2), and 0.82 (2), anterodistal angle with 3 spines, posterior margin has single smaller spines at 0.06, 0.12, 0.22, 0.35, 0.42, 0.54, 0.72, 0.83, and 0.96; ischium with a single spine at the anterodistal angle; merus broadening distally, anterior margin with 4 groups of strong spines, posterior margin with 2 smaller spines, posterodistal angle with 3 spines; carpus narrower than merus, subrectangular, anterior margin with spines at 0.17 (1), 0.29 (2+1), 0.52 (1+1), 0.60 (1), 0.78 (0+1), and 0.85 (2+1), posterior margin with 2 smaller spines, posterodistal angle with 1 large and 1 small spine; propod longer and narrower than carpus, narrowing slightly distally, anterior margin has spines at

0.15 (0+1), 0.23 (2), 0.37 (2), 0.51 (2), 0.68 (2+1), and 0.83 (2+1), posterior margin has spines at 0.25 (0+1), 0.40 (1), 0.58 (1), and 0.85 (1+1), posterodistal angle spined. Peraeopod 4: basos ovoid with 10 groups of larger spines on anterior margin, and 10 groups of smaller spines on the posterior margin; ischium rhomboidal with spines at the anterodistal angle; merus broadening distally, anterior margin with spines at 0.12 (0+1), 0.23 (2), 0.33 (0+2), 0.45 (1), 0.49 (1), 0.61 (0+2), and 0.7 (2), anterodistal margin with 1 large and 2 smaller spines, posterior margin with three spine groups, posterodistal angle with 2 large and 1 small spine; carpus narrower than merus, broadening distally, anterior margin with spines at 0.19 (0+2), 0.36 (2), 0.51 (0+2), 0.61 (1), 0.64 (3+1), 0.82 (1), and 0.92 (1), anterodistal angle with 3 spines, posterior margin with spines at 0.37 (0+1), 0.53 (1), and 0.75 (2), posterodistal margin with 4 larger spines; propod long, narrowing distally, anterior margin with 8 spine groups of 1 and 3 spines each, posterior margin with 7 spine groups of 3 spines each, posterodistal angle with 3 smaller spines. Peraeopod 5: basos greatly produced especially posteriorly, narrows a little distally, anterior margin with 10 groups of smaller spines, posterior margin with about 12 very small spines, ischium rhomboidal, spined at anterodistal angle; merus slightly broader distally, anterior margin has spines at 0.12 (2), 0.27 (2+1), 0.37 (0+3), 0.50 (2+2), and 0.75 (1+1), anterodistal angle has 3 spines, the posterior margin has spines at 0.15 (0+2), 0.30 (1+1), and 0.60 (1+1), posterodistal angle has 3 spines; carpus broadens a little distally, anterior margin has spines at 0.15 (2), 0.30 (2), 0.44

(1), 0.55 (3), 0.75 (1), 0.88 (1), and 0.92 (1), anterodistal angle has 2 large and 1 small spine, posterior margin has spines at 0.37 (1), 0.52 (1+1), and 0.73 (1+1), posterodistal angle with 3 spines; propod slightly curved, anterior angle spined at 0.13 (2), 0.23 (3), 0.38 (3), 0.54 (3), 0.65 (3), 0.77 (2), and 0.85 (3), posterior margin has spines at 0.14 (1), 0.22 (3), 0.35 (3), 0.52 (3), 0.66 (3), 0.78 (3), and 0.93 (3), posterodistal angle has a tuft of 3 spines; dactyl comparatively long, curved, with a small spine on posterior margin and a longer one on the anterior margin at base of terminal spine.

Pleopods all present and biramous, all are narrow and slender and sparsely setose; each has a pair of coupling spines (retinaculae), and the inner rami of each is the longer; segmentation of the rami is somewhat indistinct; the first and second pleopods are almost equal in length while the third is the shortest.

Epimeral plates: first, subtriangular anteroventral margin convexly curved and thickened, posterior margin with two small spines directed posteriorly; second and third subrectangular with anterior and ventral margins thickened, anterodistal angle rounded, posterodistal angle acute, posterior margin with 2 small spines.

Uropod 1: long and comparatively slender, peduncle with a row of spines on each dorsal margin, inner row terminates distally with a single long spine, inter-ramal spur very short, both rami spined dorsally, outer ramus with 8 marginal dorsal spines and 1 large, 2 medium and 1 smaller terminal spines, the larger of these terminal spines is scionate; the inner ramus has 11 dorsal marginal spines and 2 large and 2 smaller scionate terminal spines. Uropod 2: dorsal margin of peduncle with 4 spine groups, both rami spined dorsally, inner ramus terminates with 3 large spines, of which the 2 smaller are scionate, the outer ramus terminates with 1 large and 1 small spine. Uropod 3: peduncle with 3 spines, uniramate, the single ramus has one marginal spine dorsally and 3 terminal spines. Telson: moderately cleft with 4 marginal spines.

Female:

Length 20.6 mm, width 3.8 mm, depth 2.9 mm. Pigmentation pattern: very faint in type, the last 2 thoracic segments and all the abdominal segments have a reddish stripe running around the posterior margin of the dorsal aspect down to a point about 0.33 down the lateral aspect; from the mid-dorsal posterior margin a red stripe runs forward, a yellowish-white spot is defined on each side of the dorsal midline in the posterior third of each of these segments. The last 2 abdominal segments also have ill-defined spots anterioriad. Antenna 1: length 1.25 mm, with 8 podomere segments in flagellum; peduncle segment 1 with 2 spine groups on dorsal margin, spined on inferodistal angle; segment 2 with a group of 3 spines at 0.66 on dorsal margin, 1 spine at 0.33 on ventral margin, spined on inferodistal angle; segment 3 the longest and narrowest, with 1 spine at 0.5 on dorsal margin, and 4 spines on ventral margin, anterodistal angle with 2 longer spines, inferodistal angle with a short row of 4 spines. Antenna 2: length 8.5 mm, segment 3 with spines on distal margin; segment 4 has 3 spines on ventral margin, 3 spines in an axial row on the lateral face, and 1 spine on dorsal margin, inferodistal angle with 4 spines, superodistal angle with 1 spine; segment 5 has 5 spines on ventral margin, 10 spines on dorsal surface and 7 spines on lateral surface; flagellum has 22 peduncle segments.

Gnathopod 1: basos anterior margin with 5 sets of single spines, posterior margin with 3 spines at posterodistal angle; ischium with one spine on posterior margin and with 4 spines at posterodistal angle; merus posterior margin convex with about 10 spines; carpus anterior margin slightly concave with 3 spines, posterior margin produced into a scabrous lobe surrounded by numerous large spines; propod widens distally, anterior margin with 3 spine groups, anterodistal angle with about 4 large spines, posterior margin produced into a slight scabrous pellucid lobe protected by 2 parallel axial rows of large spines, palm is convex and fringed with spines; dactyl shorter than propod width, curved to conform with palm, inner surface with 2 spines, base of terminal spine with 2 small lateral spines.

Gnathopod 2: brood plate narrower proximally and distally than medially, with 23 long spines; basos produced to form a wide flat plate, ischium comparatively long; merus posterior margin produced distally to form a small pellucid lobe; carpus posterior margin forms pellucid lobe fringed at the base by a row of large spines; propod mitten-shaped, with the posterior margin produced to a large pellucid lobe which extends distally beyond the palmar area, 2 rows of spines run mid-axially on frontal and abfrontal surface, palm short and oblique, fringed by a spine row; dactyl short.

Peraeopod 1: brood plate long, square distally, setae long, not curl-tipped; like male posterior surface (ventral) more heavily spined than other surfaces, especially the merus, carpus and propod. Peraeopod 2: brood plate also square-tipped, with 21 long spines without curl tips; basos anterior margin with spines at 0.58 (1), 0.62 (1), 0.71 (1), and 0.92 (2), posterior margin has spines at 0.34 (1), 0.48 (1), and 0.65 (1), posterodistal angle with 2 large and 1 small spine; merus posterior margin with 3 groups of stout spines at 0.16 (2), 0.36 (2+1), and 0.62 (1+1), with 3 spines at posterodistal angle; propod posterior margin spined at 0.16 (1), 0.28 (1+1), 0.38 (1+1), 0.48 (2), and 0.66 (1+2), posterodistal angle with 4 spines. Peraeopod 3: ischium with 1 large and 1 small spine at the anterodistal angle; merus posterior margin with 2 larger and 2 smaller spines, posterodistal angle with 4 spines; carpus anterior margin with 3 groups of spines at 0.08 (1), 0.22 (3+2), 0.45 (1), 0.51 (3), 0.76 (1+1), 0.85 (2+1), and 0.92 (1), posterodistal angle with 1 large and 2 small spines. Peraeopod 4: sideplate rounded with no anterodistal or posterodistal angles, ventral margin with 4 minute spines; basos expanded but more square than in male due to the posterior margin being straighter, posterior margin with 12 groups of smaller spines; merus anterior margin with spines at 0.15 (2), 0.25 (2), 0.38 (2), 0.48 (2), 0.54 (1), 0.65 (2), 0.70 (1), 0.76 (1), and 0.81 (1), anterodistal angle with 3 larger spines, posterodistal angle with 2 larger and 2 smaller spines; carpus anterior margin with spines at 0.10 (2), 0.23 (4), 0.39 (2), 0.48 (3), 0.67 (3), and 0.84 (3+1), posterior margin with spines at 0.24 (1), 0.38 (1+1), 0.56 (1+2), and 0.75 (3); propod slightly curved anteriorly, anterior margin with 10 spine groups, posterior margin with 8 spine groups. Peraeopod 5: gill large and trilobed; basos posterior margin with about 16 small spines; merus anterior margin has spines at 0.09 (1), 0.18 (2), 0.27 (2+1), 0.45 (3+1), 0.59 (0+1), and 0.65 (3), anterodistal angle has 5 large spines, posterior margin has spines at 0.18 (1), 0.27 (0+2), 0.52 (1+1), 0.61 (1+1), and 0.75 (1), posterodistal angle has 4 spines; carpus anterior margin has spines at 0.16 (2), 0.32 (2+2), 0.46 (2), 0.58 (2+2), 0.75 (2), and 0.89 (2), posterior margin has spines at 0.31 (1), 0.44 (1), 0.58 (2), and 0.77 (2); propod anterior margin has spines at 0.14 (2), 0.20 (2), 0.30 (2+1), 0.42 (2+1), 0.54 (2+1), 0.63 (2+1), 0.72 (2+1), 0.82 (2+1), and 0.93 (2+1), posterior margin has spines at 0.11 (1), 0.20 (1), 0.24 (2), 0.39 (2), 0.52 (2), 0.59 (1), 0.78 (2), 0.80 (1), and 0.89 (2).

Uropod 1: as for male but inter-ramal spur very short and stout; inner ramus has two marginal rows of spines, the inner row consists of 3 spine groups at 0.57 (1), 0.67 (1), and 0.74 (2), the outer row is of 10 spines which extend from 0.32 to 0.90; the outer ramus has 8 spines arranged in a row along the dorsal margin from 0.15 to 0.77. Uropod 2: outer ramus with 8 spines in a row on the dorsal margin, inner ramus with 4 spines on the dorsal margins.

Remarks

This very distinctive New Zealand landhopper must be rare or have a very limited distribution since it has been collected only three times from a very restricted area at mid-altitudes on Mt Egmont. Other talitrid species occur at higher and lower altitudes on Mt

Egmont, but it has not been collected with these other species, suggesting that either it is the only species in the restricted area in which it occurs, or it occupies an unusual habitat not occupied by other species. It can certainly climb since it was collected by beating cabbage trees (Cordyline indivisa) by K.J.Fox. Climbing at night is not an unusual habit in New Zealand landhoppers but presumably Fox's collection was made during the day time. Perhaps, then, this species spends much of its time under bark and in the foliage like many landhoppers in tropical rain forests.

The marked differences in spination between the holotype male and allotype female should be interpreted with caution. Some of the difference is due to sexual dimorphism, but much is due to the different ages of the two specimens. As they get older amphipods add more spine groups and add more spines to existing spine groups. Since the female allotype is probably 2 instars older than the holotype male it is more spiny. A further complication is that individual spines can get broken. Thus the spination pattern will differ in detail from individual to individual depending on age and the actual life experiences of the individuals concerned. This variability may make it appear that spination patterns are too variable to be of much use in taxonomy, but this is not so. Provided they are interpreted with due consideration for the sources of variation mentioned above, spination patterns can be of great value in species recognition, especially in feminized species, that is species with little sexual dimorphism.

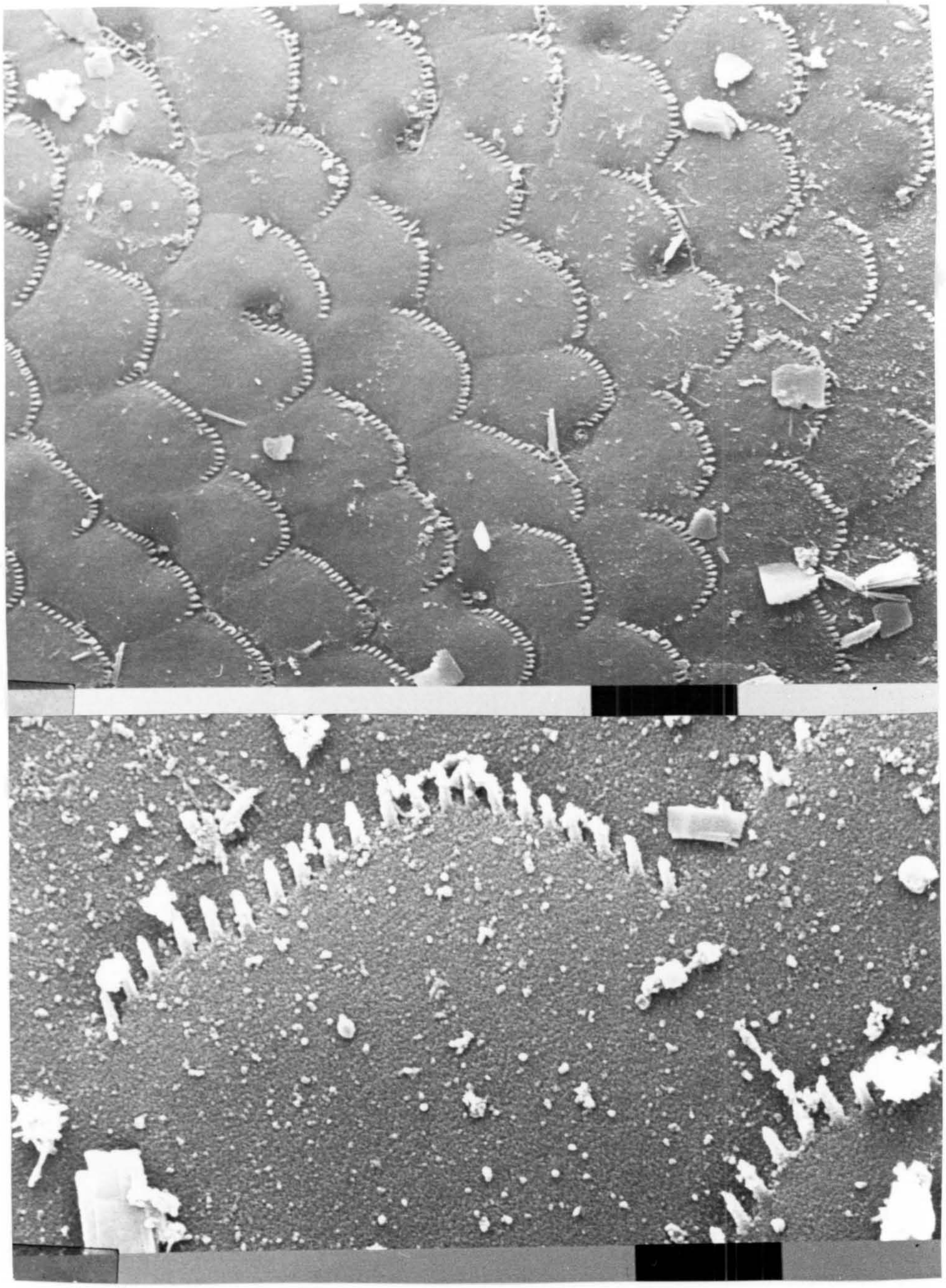


FIGURE 201. Cuticular structures in Tara sinbadensis. The mesopores are arranged in arcs and have long fingers or 'verandas'. Macropores are also numerous.

Tara hauturu new species

Figures 202 to 219.

Types:

Holotype male and allotype female: Little Barrier Island, G.W.Ramsay, 23-28/XI/1954, deposited in the Canterbury Museum (Author's catalogue no. KD 647).

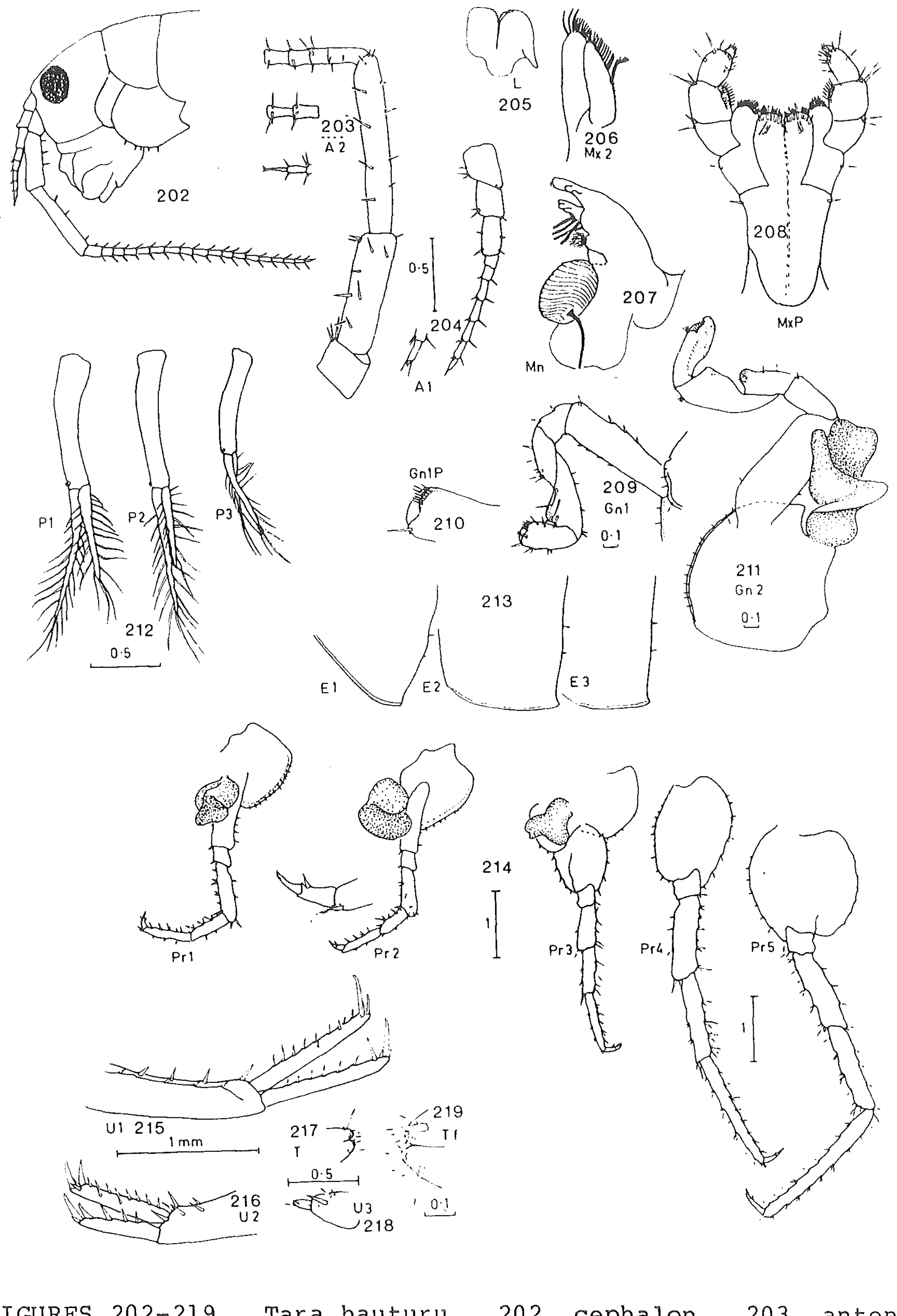
Etymology: the specific epithet is from the Maori name for Little Barrier Island, hauturu, which means 'wind's resting post' (Reed and Brougham, 1978).

Localities and collectors:

Little Barrier Island 23-28/XI/1952, G.W.Ramsay, 2 large males and 1 larger female, 4 smaller females, taken with 1 large specimen of *Talitroides topitotum*. Little Barrier Island, 1/III/1948, R.A.Falla, in leaf mould, small specimens taken with *Talorchestia aotearoa* and *Parorchestia tenuis*.

Diagnosis:

A moderately sized, weakly sexually dimorphic landhopper of the genus *Tara*, eyes oval, black, antenna 1 extends to just beyond the end of antenna 2 peduncle segment 5, of 8 flagellar podomere segments; antenna 2 moderately long, with 21 flagellar podomere segments; mandible with only 4 interdentate pilose setae and a prominent abmolar setal tuft; maxilla 2 plates foliaceous;



FIGURES 202-219. Tara hauturu. 202, cephalon. 203, antenna 2. 204, antenna 1. 205, lower lip. 206, maxilla 2. 207, mandible. 208, maxilliped. 209, gnathopod 1. 210, gnathopod 1 propod. 211, gnathopod 2. 212, pleopods 1,2 & 3. 213, epimeral plates 1,2 & 3. 214, peraeopods 1,2,3,4 & 5. 215, uropod 1. 216, uropod 2. 217, telson male. 218, uropod 3. 219, telson female.

gnathopod 1 chelate in both sexes; gnathopod 2 mitten-shaped in both sexes; gills moderately large, first and last trilobed, last with a relatively short pendulous lobe; pleopods all present and biramous, segmentation on rami not obvious, 2 coupling spines present on inner margin of peduncle, peduncle inner margins naked; uropod 1 long, rami heavily spined dorsally, inner ramus with a second row of dorsal spines, inter-ramal spine absent; second uropod rami heavily spined dorsally, inter-ramal spur present; telson moderately cleft with 1 long submarginal and 4 marginal spines on each lobe.

Description:

Male:

Length 10.88 mm, width 1.90 mm, depth 1.95 mm. Eye black, ovoid with long axis at 46° to longitudinal axis, length of long axis of eye 1.33 length of short axis. Cheek rounded with 3 long marginal spines. Antenna 1: length 1.65 mm; extends to just beyond end of antenna 2 peduncle penultimate segment; peduncle segment 1 superior margin naked, superodistal angle with 1 spine, inferior margin with 1 spine midway, inferodistal angle with 2 spines; segment 2 narrower than segment 1, and narrowing distally, superodistal angle with 1 spine, inferodistal angle with 2 spines; segment 3 narrower and slightly longer than segment 2, both margins slightly scalloped, superior margin spined at 0.50, superodistal angle with 1 spine, inferior margin spined at 0.45, inferodistal angle with 2 spines; flagellum tapering, of 8 podomere segments, the proximal segments are the shortest and broadest, becoming progressively longer and narrower distally; each podomere segment except 1, 7 and 8 has 1 spine at superodistal angle and 2 oblique spines at the inferodistal angle; first segment is naked; penultimate segment is comparatively long and tapering, last segment is a short stump bearing a close-bound terminal tuft.

Antenna 2: length 6.13 mm; moderately long and tapering; peduncle segment 3 short, distal margin with 4 or 5 spines inferiorly; segment 4 broadening slightly distally, superodistal angle has 1 spine, lateral face has 3 spines and inferior surface has 2 rows of 3 spines each, distal margin has 5 spines inferiorly; segment 5 long, broadening distally, superior margin spined at 0.14, 0.29, 0.39, 0.59, 0.73, and 0.88, lateral face spined 0.21 (2), 0.39 (2), 0.64 (2), and 0.82 (2), inferior margin spined at 0.21, 0.38, 0.63, and 0.79, outer distal margin with 5 large spines; flagellum moderately long and tapering, of 21 podomere segments, each of which broadens only slightly distally and has a pair of spines at each of the 4 distal angles, last segment long with a short, sparse terminal tuft of setae.

Mouthparts: Upper lip: ventral margin rounded, setose, inner shelf present, setose. Mandible: maxilla 5-toothed, lacinia mobilis 4-toothed, 4 interdentate pilose setae, abmolar setal tuft dense and prominent, molar 18-striate, molar medial setae pilose and longer than molar width. Lower lip: ventral margins subsquare, setose only on inner region of distal margin and on inner margin. Maxilla 1: outer plate subrectangular, outer margin slightly sinuous, distal margin rounded, bears 9 inwardly-curved spine teeth with 0, 0, 1, 1, 2, 2, 2, 2 lateral teeth (from outer to inner),

inner plate narrow, narrowing distally, inner margin pilose, distal margin bears 2 long pilose setae. Maxilla 2: both plates foliaceous; outer plate outer margin convex, sparsely pilose, distal margin rounded, bearing a row of 13 inwardly-curved setae of which the 3 outer spines are larger than the rest, inner margin nearly straight; inner plate outer margin convex, distal apex rounded, inner margin with 17 setae from distal to medial where the spine row terminates with a densely pilose, long seta, proximal outer margin sparsely pilose.

Gnathopod 1: plinthic ridge present with 5 marginal spines; basos broadening distally, anterior margin with small spines at 0.55, 0.65, 0.74, 0.86, and 0.92, posterior margin slightly scalloped between spines at 0.46 and 0.61, posterodistal angle with 1 spine; ischium anterior margin not produced, posterior margin with 1 spine midway, posterodistal angle with 2 spines; merus posterior margin rounded but not produced, with 7 spines; carpus anterior margin convex, slightly scalloped, spined at 0.31, 0.42, 0.53, and 0.69, anterodistal angle with 4 spines, posterior margin produced into a pellucid angle with 4 spines, posterior margin produced into a pellucid lobe distally, protected by 6 large submarginal spines and 3 mesial spines; propod broadening distally, length twice width, anterior margin stepped, spined at 0.52 and 0.76, anterodistal angle with 2 long spines, posterior margin with long spines at 0.45, 0.65, and 0.79, a row of 3 to 4 spines runs longitudinally on the inner face, palm convex, 0.5 propod width, flanked by 2 large spines at anterior end, 5 smaller spines medially, and 5 larger spines posteriorly, palmar angle about 105°, dactyl slightly shorter than propod width, outer margin naked.

Gnathopod 2: coxal plate ventral margin rounded, with about 15 spines; gill large, subcranial lobe long and narrow; basos length twice width, narrowing slightly distally, anterior margin sinuous, spined at 0.32 and 0.85, posterior margin slightly convex, spined at 0.30, 0.56, and 0.82; ischium posterodistal angle with 2 spines; merus posterior margin convex, produced into a discrete pellucid lobe distally, spined at 0.30, 0.50, 0.65, 0.86 and 0.92; carpus broadening distally, anterior margin naked, anterodistal angle with 2 spines, posterior margin produced into a pellucid lobe which broadens distally, posterodistal angle with 2 spines; propod long and narrow, width 0.19 mm, length 0.57 mm, margins naked, anterodistal margin with 4 spines, posterior margin produced into a lobe which extends beyond palmar area, palm short, oblique, flanked by 9 spines, palmar angle 33^{o}; dactyl length about 0.5 propod width, curved so that its distal end appears to occlude the propod distal lobe.

Peraeopod 1: coxal plate subsquare, anterodistal angle rounded, ventral margin convex, with 14 marginal spines; gill large though smaller than gnathopod 2 gill, discoidal, half-spiralled; basos narrowing slightly distally, curved slightly anteriorly, anterior margin concave, with small spines at 0.59, 0.69, and 0.77, posterior margin with larger spines at 0.49, and 0.70, posterodistal angle with 2 spines; ischium anterior margin slightly produced anteriorly, posterodistal angle with 2 spines; merus broadening distally, anterior margin convex, slightly stepped, spined at 0.28, and 0.51, anterodistal angle with 2 spines, posterior margin slightly scalloped, spined at 0.36, 0.62, and 0.76, posterodistal angle with 2 spines; carpus curved slightly posteriorly, both margins stepped, anterior margin spined at 0.36 and 0.56, anterodistal angle with 1 spine, posterior margin spined at 0.19 (1), 0.40 (3), 0.61 (3), 0.85 (2), ad 0.92 (1), posterodistal angle with 2 spines; carpus narrowing slightly distally, curved posteriorly, both margins stepped, anterior margin spined at 0.25 (2), 0.49 (2), and 0.75 (3), anterodistal angle with 3 spines, posterior margin spined at 0.18 (3), 0.30 (3), 0.48 (3), 0.65 (3), and 0.85 (3); dactyl conical, curved posteriorly, with 1 long spine on posterior margin at base of terminal spine.

Peraeopod 2: coxal plate ventral margin nearly straight, with about 11 spines; gill large, discoidal, folded in type; basos curved anteriorly, anterior margin concave, naked, anterodistal angle with 1 spine, posterior margin spined at 0.23, 0.38, and 0.63 (2), posterodistal angle with 1 spine; ischium posterodistal angle with 1 spine; merus broadening distally, anterior margin convex, spined at 0.28 and 0.50, anterodistal angle with 2 spines, posterior margin slightly sinuous, spined at 0.15, 0.35 (2), and 0.57, posterodistal angle with 2 spines; carpus length 0.67 merus length, anterior margin stepped, spined at 0.52, anterodistal angle with 1 spine, posterior margin scalloped, spined at 0.14 (1), 0.29 (3), 0.57 (1), and 0.72 (3), posterodistal angle with 2 spines; propod narrowing slightly distally, curved posteriorly, anterior margin stepped and scalloped, spined at 0.22 (1), 0.43 (2), and 0.70 (3), anterodistal angle with 3 spines, posterior margin stepped, spined at 0.25 (3), 0.40 (3), 0.59 (3), and 0.78 (3), posterodistal angle with 2 spines; dactyl curved posteriorly, inner margin with a spine distally, emarginate proximally, bearing a short protruberance between marginal spine and terminal spine, outer margin smoothly convex, with a minute spine at the base of the terminal spine.

Peraeopod 3: coxal plate: both lobes with about 5 spines; gill small, discoidal; basos an inverted pyriform shape, anterior margin with 7 large spines, posterior margin with 7 slightly smaller spines; ischium anterodistal angle with 1 spine; merus broadening distally, both margins scalloped, anterior margin spined at 0.26 (2), 0.47 (2), and 0.70 (1), anterodistal angle with 3 spines, posterior margin spined at 0.27 (2), 0.34 (1), and 0.52 (2), posterodistal angle with 3 spines; carpus length equals merus, anterior margin scalloped, spined at 0.33 (3), 0.58 (3), and 0.87 (3), posterior margin stepped, spined at 0.44 (2) and 0.71 (2), posterodistal angle with 3 spines; propod narrowing distally, both margins stepped, anterior margin spined at 0.22 (2), 0.35 (2), 0.53 (3), 0.67 (3), and 0.84 (3), posterior margin spined at 0.32 (1), 0.52 (1), and 0.76 (2), posterodistal angle with 2 spines; dactyl curved inwardly, inner margin smoothly concave, with one spine distally, and a protuberance between the marginal spine and the base of the terminal spine.

Peraeopod 4: gill large, trilobed, pendulous lobe not very long, triangular; basos ovoid, width 0.65 length, anterior margin with 8 spines, anterodistal angle with 2 spines, posterior margin with 11 spines; ischium anterodistal angle with 1 spine, posterior margin sinuous; merus broadening slightly distally, anterior margin stepped and scalloped distally, spined at 0.11 (1), 0.22 (2), 0.34

(2), 0.46 (3), 0.61 (2), and 0.70 (3), anterodistal angle with 4 spines, posterior margin stepped, spined at 0.24 (1), 0.39 (1), and 0.74 (2), posterodistal angle with 2 spines; carpus margins subparallel, anterior margin scalloped and stepped, spined at 0.19 (3), 0.36 (3), 0.59 (3), and 0.78 (2), anterodistal angle with 3 spines, posterior margin stepped and scalloped distally, spined at 0.23 (1), 0.35 (2), 0.53 (3), and 0.76 (3), posterodistal angle with 3 spines; propod narrowing slightly distally, anterior margin stepped, spined at 0.15 (2), 0.26 (2), 0.39 (3), 0.50 (2), 0.59 (3), 0.71 (2), 0.80 (2), and 0.91 (3), posterior margin stepped and scalloped, spined at 0.17 (1), 0.29 (2), 0.46 (2), 0.57 (1), 0.66 (2), 0.74 (1), and 0.94 (2), posterodistal angle with 3 spines; dactyl conical.

Peraeopod 5: basos nearly circular, width 0.95 length, anterior margin with 10 spine groups, anterodistal angle with 2 spines, posterior margin scalloped, stepped, with 9 minute spines; ischium anterodistal angle with 3 spines; merus margins subparallel, anterior margin scalloped and stepped, spined at 0.10 (2), 0.23 (2), 0.37 (3), 0.52 (4), and 0.73 (2), anterodistal angle with 4 spines, posterior margin spined at 0.19 and 0.44 (1+1), posterodistal angle with 2 spines; carpus margins subparallel, anterior margin scalloped, spined at 0.21 (2), 0.35 (2), 0.49 (1), 0.59 (4), and 0.81 (2), anterodistal angle with 5 spines, posterior margin stepped, spined at 0.22 (1), 0.33 (1), 0.48 (2), and 0.71 (2), posterodistal angle with 2 spines; propod narrowing distally, curved anteriorly, anterior margin stepped, with 2 spines at each of 0.16, 0.25, 0.38, 0.49, 0.58, 0.70, 0.77, 0.86, and 0.94, anterodistal angle with 1 spine, posterior margin stepped, spined at 0.09 (2), 0.15 (3), 0.27 (2), 0.43 (3), 0.53 (2), 0.56 (2), 0.73 (3), 0.83 (3), and 0.93 (3); dactyl long and conical.

Pleopods: First and second: length 1.88 mm; narrow, delicate, peduncle margins naked except for 2 coupling spines on inner distal margin; both rami present; outer ramus shorter than inner; inner ramus slightly longer than peduncle, both margins on both rami with long setae, segmentation not obvious. Third: slightly more reduced, length 1.35 mm, peduncle margins naked except for 2 coupling spines on inner distal margin; outer ramus shorter than inner, both rami margins with long setae, segmentation even less obvious than with pleopods 1 and 2.

Sideplates: First: subtriangular, posterior margin emarginate distally to form a notch at acute posterodistal angle, with 2 backward-pointing spines proximally. Second and third subsquare, ventral margins only slightly convex, posterior margin notched near acute posterodistal angle, with 2 backward-pointing spines proximally.

Uropod 1: relatively long and delicate, heavily spinose with long spines; ramus with 2 rows of 4 spines each dorsally, no inter-ramal spur; outer ramus with 6 marginal spines dorsally, terminates with 2 long and 2 short spines; inner ramus with 1 row of 8 spines on inner dorsal margin and a row of 2 spines on outer dorsal margin, terminates in 1 very long, 1 long and 2 shorter spines. Uropod 2: peduncle with 5 dorsal spines, inter-ramal spine present; outer ramus with 3 marginal dorsal spines, a 2 long and 1 short terminal spine; inner ramus heavily spined with 8 spines on the inner dorsal margin, 2 spines on the outer dorsal margin, and 2 larger and 2 smaller terminal spines. Uropod 3: uniramate; peduncle with 4 dorsal spines; ramus with 1 long and 1 short terminal spine. Telson: bilobed, but not deeply cleft, with 1 long spine towards outer margin, and 3 shorter spines medially.

Female: As for male except where specified:

Length 12.3 mm, width 17.8 mm, depth 2.14 mm. Antenna 1 peduncle segment 2 with 1 spine on superior margin at 0.5; peduncle of 6 segments. Antenna 2 flagellum with 18 podomere segments. Gnathopod 1: sideplate ventral margin rounded with 6 large spines; propod anterodistal angle with 3 large spines; dactyl terminates slightly short of propod ventral margin. Ganthopod 2: basos narrower; broodplate in nonbreeding condition. Peraeopods: broodplates in nonbrooding condition. Uropod 1: outer ramus with 4 dorsal marginal spines; inner ramus with 1 row of 7 spines on inner dorsal margin, and 1 spine on outer dorsal margin. Uropod 2: outer ramus with 2 spines on dorsal margin, inner ramus with 7 spines. Telson: bilobed, not deeply cleft, each lobe has 1 large spine submarginally, and 4 smaller marginal spines.

Remarks

Tara hauturu is readily identified by the heavily spined uropods which are very distinctive. In most other species the outer rami of the uropods tends to be naked or only weakly spined. *T.hauturu* probably has a wider distribution than that recorded, but it may be confused with females of <u>T.sylvicola</u>, which itself was overlooked for 130 years even though they are very common.

Genus *Waematau* new genus

Diagnosis:

Like *Tara* with pleopod peduncle margins without stout setae, broodplates long and delicate, spined only distally, uropod 1 outer ramus naked, uropod 2 both rami spined; many species with pleopods reduced, especially third or second and third pairs.

Etymology: from the Maori for 'foot' and 'hook' an allusion to the large inter-ramal spur present in most species in this genus.

Type species: *Waematau* *triregis* new species.

Other species: *W.unuwhao* new species, *W.espiratus* new species, *W.kaitaia* new species, *W.reinga* new species.

Remarks

The genus *Waematau* is confined to Northland. It contains some very apomorphic species including some feminized ones. It is likely that the group speciated in a reticulate manner fairly recently (for landhoppers) from a common ancestor in Northland, in response to the extensive geological and geomorphological events which have occured there and which are still occurring. One is tempted to coin the term 'speciation playground' for this area of thousands of islands, false islands, emerged island chains and volcanism which has caused repeated isolation of populations and thus extensive speciation. Many of the species in Northland are local to a range of mountains or even single coastal hills, which suggests that they originated when these features were isolated islands, and have not dispersed from their region of origin.

No doubt there are more species yet to be found if they have survived the massive habitat destruction and alteration caused by man. Some of the species described herein may have become extinct already since I have been unable to locate them in their type locality from where they were collected a few years ago by other people.

Waematau triregis new species

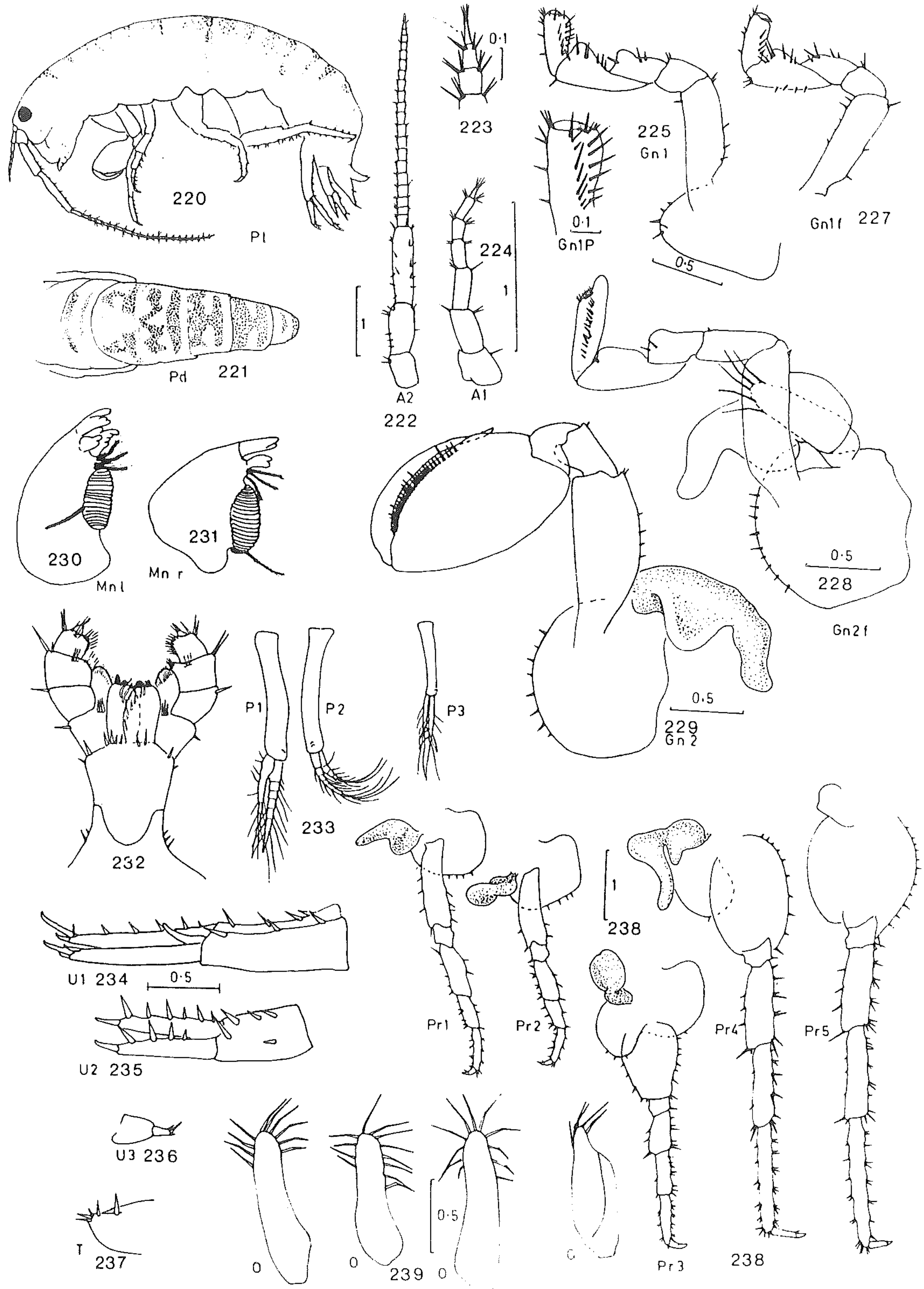
Figures 220 to 240.

Types:

Holotype male and allotype female: Summit, 200 m, Three Kings Island, 28/XI/1970, coll. G.Kuschel, deposited in the Canterbury Museum . (Author's Catalogue No. KD 916).

Localities and collectors:

Headquarters Rd., beside river, Waipoua Forest, B.M.& V.A.May, 15/XII/1976, litter, 76/105 (KD 867, 868). Forest remnant, Pekerau, 91 m, Kaingaroa area, K.A.J.Wise, 8/VII/1967, in puriri leaf litter, found with *Talitroides topitotum* and *Parorchestia tenuis* (KD 874). Cascades Kauri Park, Waitakere Range, J.C.Watt, 14-17/X/1976, pit traps, taken with *T.topitotum* (KD 895). ND Manganuka Summit 386 m, B.M.May, 13/XII/1976, litter, taken with *Tara sylvicola* (KD 903). Summit, Three Kings Island, 200 m, G.Kuschel, 28/XI/1970, litter. Summit Ridge, South West Island, Three Kings Group, E.G.Turbott, 13/I/1951, (Au P/S 4, KD 833). Butterfly Valley, Tauranga Bay, Whangaroa County, K.A.J.Wise, 28/XI/1966 (Au P/S 43, KD 834). Omahuta, S.F. N.D., J.C.Watt, 10/X/1974, regeneration after clear-felling near kauri reserve, taken with *T.sylvicola*, *P.tenuis* and *T.topitotum* (ED 74/79, KD 863). Omahuta Kauri Reserve, J.C.Watt, 10/X/1974, litter, taken with *Talorchestia aotearoa* (ED 74/81, KD 865). Waipoua Forest, R.R.F., 6/I/1967.



FIGURES 220-239. Waematau triregis. 220, lateral aspect. 221, dorsal aspect. 222, antenna 2. 223, antenna 2 distal. 224, antenna 1. 225, gnathopod 1. 226, gnathopod 1 male propod. 227, gnathopod 1 female. 228, gnathopod 2 female. 229, gnathopod 2 male. 230, left mandible. 231, right mandible. 232, maxilliped. 233, pleopod 1,2 & 3. 234, uropod 1. 235, uropod 2. 236, uropod 3. 237, telson. 238, peraeopods 1,2,3,4 & 5. 239, oostegites.

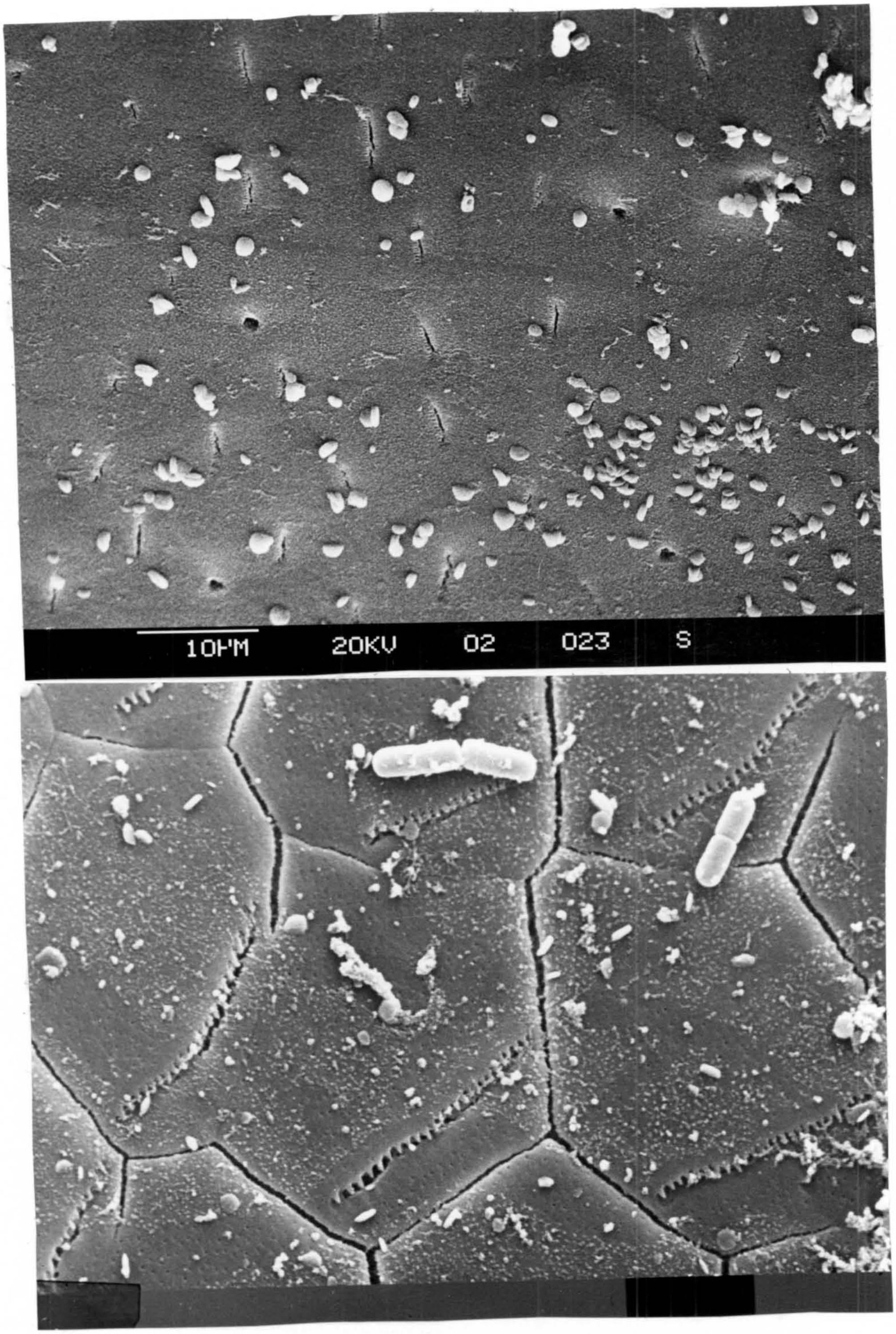


FIGURE 240. Cuticular structure of Waematau triregis. The upper micrograph shows the dorsal surface of abdominal segment 2. A large mesopore opens in a dermal gland polygon. The polygon boundaries are well defined even though much mucoid material was present on the specimen. The mesopores are arranged in a slit near the posterior margin(s) of the polygons and are overhung by 'verandas'. The lower micrograph is of the midlateral surface of the last abdominal segment. The mesopore slits are nearly straight and the 'verandas' are marked. Note the presence of cells on the surface, possibly coliform bacteria. The scale bar on the lower micrograph indicates 3.7 micrometres.

Etymology: the name is derived from the Latin for three kings, the type locality, modified for euphony.

Diagnosis:

A large, strongly sexually dimorphic landhopper of the genus Waematau, with large eyes, medium sized slender antenna 2, antenna 1 extends to 0.33 along antenna 2 peduncle segment 5, gnathopod 1 chelate in both sexes, male gnathopod 2 strongly subchelate with the propod and elongated ovoid having a convex palm heavily spined and a long, overlapping dactyl with a 'soft' tip; female gnathopod 2 mitten-shaped; broodplates reduced with only a few brood spines, the fourth broodplate is rolled with few spines; gills of moderate size, discoidal; uropod 1 long, outer ramus naked; uropod 2 both rami equal and spined; telson with only few marginal spines, pleopods all present and biramous though third smaller than anterior two pairs.

Description:

Male:

Length 13.8 mm, width 2.82 mm, depth 2.65 mm. Body not very deep. Pigmentation pattern in alcohol of the partly reticulated type. Head deeper than long. Eye round, black, about 0.33 head length. Antenna 1: length 1.50 mm, extends to 0.33 along antenna 2 peduncle segment 5; peduncle segment 1 narrowing distally, with 1 large spine at 0.66 on inferior margin; second segment longer than first but narrower, superior margin straight, inferior margin convex, spined only at superior distal angle and 0.75 on inferior margin; third segment slightly shorter than second and narrower, margins parallel, spined at distal angles; flagellum short, of 4 segments, each with 3 large spines at superior and inferior distal margins; podomere segment 2 shorter than 3, terminal cluster of spines as long as ultimate segment, not close bound. Antenna 2: length 5.42 mm; segment 3 narrower than segment 4, with a pair of spines on the inferodistal angle; segment 4 broadening distally, 1.5 times the length of segment 3, one small spine on mid-dorsal margin, 1 spine at superodistal angle, 3 spines on inferior margin, 4-5 spines at inferodistal angle; flagellum relatively short, not very tapering, of 21 podomere segments; podomeres with moderately long spines; terminal tuft short and sparse. Mouthparts: Upper lip: rounded distal margin densely pilose, inner shelf not well developed. Mandible: incisor 7-cuspate, lacinia mobilis 4-toothed, 6 inter-dentate pilose setae set in pairs along margin, molar 22-striate, molar medial seta present and pilose. Lower lip distal margin and inner margins pilose. Maxilla 1: inner plate slender, terminating in two long, pilose setae; outer plate broader, margins subparallel but curved inwards, distal margin with 9 stout teeth bearing 0, 0, 4, 4, 4, 4, 4, 4, 4 lateral teeth (from outer to inner). Maxilla 2: outer plate outer margin curved convexly, distal margin rounded, spined; inner plate subtriangular with distal margin spined, spine row terminating proximally on inner margin with one large pilose seta, inner margin proximal to this pilose and rounded convexly. Maxilliped: not very broad but palps broad and arcuate; palp segment 4 small, but not obscured by segment 3.

Gnathopod 1: coxal plate ventral margin rounded, with 4 spines; basos broadening immediately proximally then narrowing slightly distally, anterior margin straight, with 1 small spine at 0.69, anterodistal angle with 1 spine, posterior margin convex, with larger spines at 0.20, 0.31, and 0.49 and at posterodistal angle; ischium with 3 spines at posterodistal angle; merus longer than ischium, posterior margin produced into a pellucid lobe distally and protected by 6 stout spines around its base; carpus anterior margin convex and naked except for a spine at anterodistal angle, posterior margin produced to a prominent pellucid lobe protected by 6 stout spines at its base; propod shorter than carpus, broadening distally, anterior margin with spines at 0.38, 0.64, and 0.87, and 4 stout spines at the anterodistal angle, posterior margin somewhat produced to a pellucid lobe, with a row of 6 stout spines running longitudinally on the inner face, the outer face has two longitudinal rows, palm transverse, flanked by a short row of spines which terminate in longer spines at each end; dactyl about 3/4 propod width.

Gnathopod 2: coxal plate ventral margin rounded, with about 11 spines; gill moderately large trilobed, not plicate; basos broadening in the middle then narrowing a little distally, anterior margin straight, with one minute spine at 0.72, posterior margin convex, spined at 0.39, 0.46, 0.53, 0.61, and 0.72 and at posterodistal angle; ischium posterodistal angle spined; merus short with 1 small spine near posterodistal angle; carpus short, broadening distally; propod massively produced to an ellipsoid, broadening somewhat distally, margins naked, palm long, smoothly rounded convexly, palmar angle 150°, palm flanked by a row of about 24 spines on each side, near the termination posteriorly are two large guiding spines one on each side; dactyl very long, longer than palm, curved to conform with palm, inner surface naked, terminates in a flexible 'soft tip' which is slightly curved.

Peraeopod 1: coxal plate subsquare with rounded anterior and posterior distal angles, ventral margin only slightly convex with 10 spines; gill relatively small, simple and discoidal; basos 3.4 times longer than broad, curved anteriorly broadening a little distally, anterior margin somewhat sinuous, spined at 0.54, 0.60, 0.71, 0.81, and 0.89 (2), posterior margin convex, spined at 0.23, 0.37, 0.52, and 0.76, and at posterodistal angle (2); ischium short, anterior margin angularly produced, posterior margin straight with 2 spines at posterodistal angle; merus broadening distally, anterior margin convex, with stout spines at 0.33 and 0.55, and at anterodistal angle, posterior margin straight, spined at 0.16 (3), 0.39 (2), 0.48 (1), 0.68 (2), and 0.89 (1), and at posterodistal angle (2); carpus shorter and narrower than merus, subrectangular, anterior margin spined at 0.25 and 0.49 and at anterodistal angle, posterior margin slightly scalloped between spine groups, spined at 0.24 (1), 0.41 (1), 0.49 (3), 0.67 (1), 0.80 (1), and 0.84 (1), and at posterodistal angle (1); propod slightly longer than merus but narrower, narrowing slightly distally, anterior margin somewhat convex, spined at 0.23 (1), 0.47 (1), 0.79 (2), and at anterodistal angle (3+1), posterior margin straight, spined at 0.16 (1), 0.27 (2), 0.48 (3), 0.69 (3), and 0.87 (3), and at posterodistal angle (1); dactyl with long inner spine at base of terminal spine.

Peraeopod 2: coxal plate ventral margin straight with 7 spines, anterodistal and posterodistal angles rounded; gill simple, relatively small, discoidal; basos curved anteriorly, broadening distally, anterior margin concave, spined only at 0.71, 0.81, and 0.86, posterior margin convex, spined at 0.27, 0.38, 0.55, and 0.71; ischium posterodistal angle with 3 spines; merus broadening to a slight posterodistal bulge, anterior margin curved, spined at 0.45 and 0.64, posterior margin straight, spined at 0.24 (1), 0.45 (1), 0.69 (2), and 0.94 (2); carpus short and narrower than merus, anterior margin convex and spined at 0.42 and at anterodistal angle, posterior margin straight but somewhat scalloped between spine groups, spined at 0.34 (2), 0.52 (3), and 0.85 (3), and at posterodistal angle (1); propod narrowing distally, slightly curved posteriorly, anterior margin spined at 0.21 (1), 0.46 (2), and 0.77 (2), and at anterodistal angle (2+1), posterior margin spined at 0.21 (2), 0.37 (3), 0.57 (4), 0.78 (4), and 0.88 (1) and at posterodistal angle (1); dactyl posterior margin concave and somewhat indented or notched, anterior margin with 2 small spines.

Peraeopod 3: coxal plate posterior lobe larger than anterior, anterior lobe with 4 spines on ventral margin, posterior lobe with 6 larger spines on ventral margin; gill simple, discoidal; basos broad proximally, narrowing distally, anterior margin with stouter spines than posterior; ischium short, spined at anterodistal angle; merus broadening distally, anterior margin scalloped between spine groups, spined at 0.20 (1), 0.45 (3), 0.75 (1), 0.85 (1), and 0.96 (1), posterior margin somewhat convex, spined at 0.32 and 0.60, and at posterodistal angle; carpus narrower than merus, sides subparallel, anterior margin spined at 0.16 (2), 0.31 (3), 0.53 (3), and 0.83 (3), posterior margin spined at 0.57 and at posterodistal angle (3); propod narrowing distally, anterior margin somewhat scalloped between spine groups, spined at 0.16 (1), 0.25 (3), 0.42 (3), 0.59 (3), and 0.81 (3), posterior margin spined at 0.19 (1), 0.34 (2), 0.56 (2), and 0.81 (2), and at posterodistal angle (4); dactyl narrowing distally, but inner margins straight.

Peraeopod 4: coxal plate small and rounded distally; gill trilobed with pendulous lobe long and narrow; basos ovate, longer than broad, anterior margin with large spines, posterior margin with smaller spines; ischium with 2 spines at the anterodistal angle; merus broadening distally, anterior margin nearly straight but scalloped between spine groups, spined at 0.08 (1), 0.19 (2), 0.39 (2), 0.59 (2), and 0.86 (2), posterior margin spined at 0.19, 0.32, 0.51, and 0.70, and at posterodistal angle (2); carpus margins subparallel, anterior margin scalloped between spine groups, spined at 0.11 (1), 0.23 (3), 0.41 (3), 0.64 (3), 0.89 (3), and 0.99 (3), posterior margin with small spines at 0.20 (1), 0.34 (1), 0.47 (1), 0.61 (1), and 0.74 (2), with 3 long spines at the posterodistal angle; propod 1.5 times longer than carpus but only 0.67 times as broad, both margins slightly scalloped and stepped at spine groups, anterior margin spined at 0.08 (1), 0.15 (2), 0.25 (2), 0.41 (3), 0.58 (3), 0.74 (3), and 0.89 (3), posterior margin spined at 0.20 (1), 0.33 (2), 0.55 (2), 0.74 (3), 0.86 (3), and 0.95 (2), posterodistal angle with 3 double spines; dactyl conical, margins straight.

Peraeopod 5: basos as broad as long, anterior margin with stronger spines than posterior; ischium anterodistal angle with 3 spines; merus broadening distally, both margins somewhat scalloped and stepped though the anterior more so, anterior margin spined at 0.16 (2), 0.28 (3), 0.45 (4), 0.70 (4), and 0.95 (5), posterior margin spined at 0.10, 0.24, 0.45, and 0.65 and at posterodistal angle (2); carpus broadening a little distally, 1.1 times longer than merus but width only 0.7, anterior margin scalloped, spined at 0.13 (1), 0.19 (1), 0.25 (2), 0.40 (3), 0.60 (4), 0.79 (2), 0.90 (2), and 0.96 (2), posterior margin nearly straight, with small spines at 0.22, 0.32, 0.48, and 0.72, posterodistal angle with 2 stout spines; propod narrowing slightly distally, 1.35 times longer than carpus, both margins stepped at spine groups, anterior margin spined at 0.12 (2), 0.23 (3), 0.35 (3), 0.52 (3), 0.66 (3), 0.82 (3), and 0.94 (3), anterodistal angle with 1 small spine, posterior margin spined at 0.19 (2), 0.30 (2), 0.47 (3), 0.63 (3), 0.80 (3), and 0.97 (3), posterodistal angle with 4 spines.

Pleopods all present, slender and biramous; first 1.13 times longer than second and 1.80 times longer then third; each has 2 coupling spines, peduncle margins are naked, inner rami are longer than outer, both rami segmented on all pairs, ramal setae sparse, not pilose.

Epimeral plates: first; anteroventral margin somewhat rounded but posterodistal angle acute, not rounded, posterior margin with 2 spines; second: subsquare, anterodistal angle rounded, ventral margin somewhat convex, posterodistal angle acute, posterior margin concave and scalloped between the 6 backward pointing spines; third anterodistal angle rounded, ventral margin convex, posterodistal angle acute, posterior margin sinuous and slightly scalloped between the 4 backward pointing, minute spines.

Uropod 1: peduncle with 2 rows of 3 to 4 spines each dorsally, large inter-ramal spur present (0.43 ramus length), rami equal in length, longer than peduncle, inner with 5 spines, outer naked, both terminate 1 large and 2 smaller scionate spines; Uropod 2: peduncle with 4-5 dorsal spines; rami of equal length, very slightly longer than peduncle, both rami spined dorsally; Uropod 3: uniramous, naked except for 2 terminal spines; telson bilobed but median cleft not deep, about 6 spines marginally.

Female: as for male except where noted:

Length 13.5 mm, width 2.71 mm, depth 2.82 mm. Antenna 2 length 5.74 mm; segment 4 superior margin naked; flagellum of 21 podomere segments.

Gnathopod 1: basos anterior margin with small spines at 0.43, 0.51, 0.61, 0.74, 0.83, and 0.91, posterior margin with larger spines at 0.25 and 0.52 and 2 at posterodistal angle; carpus anterior margin with spines at 0.29, 0.40, 0.51, and 0.63, anterodistal angle with 3 spines; propod not quite as broad distally as in male, dactyl extends to propod margin.

Gnathopod 2: broodplate narrowing a little distally, setae reduced in number, basos slightly curved posteriorly, anterior margin with spines at 0.21, 0.25, 0.33, 0.43, and 0.58, posterior margin naked except for 3 spines at distal angle; ischium long, broadening distally, with 2 spines at posterodistal angle; merus produced posteriorly to a pellucid lobe protected by 2 spines on each surface; carpus long, anterior margin naked except for 2 spines at distal angle, posterior margin produced to a pellucid lobe protected by a row of 3-4 spines mesially on outer face, 2 spines at posterodistal angle; propod long, narrow and mitten-shaped, with about 20 large spines running longitudinally and submesially on both outer and inner faces, palm short, palmar angle 38^{o}, palm flanked by a row of short setae, posterior margin of propod extends well beyond palm termination to a soft pellucid lobe into which the short dactyl occludes.

Peraeopod 1: broodplate short, narrowing distally, sparsely setose, distal margin rounded; basos and merus more broad distally because of the more rounded and produced anterior margin. Peraeopod 2: more peg-shaped than in male; broodplate larger than that of peraeopod 1, tapering distally, sparsely setose; basos broader distally, anterior margin convex distally, spination as for male except for posterior margin at 0.71 which has 2 spines; merus broader distally; dactyl indentation not as marked. Peraeopod 3: broodplate margin thickened and rolled, distal margin rounded and narrow, about 5 terminal setae. Peraeopod 4: carpus posterior margin with spines at 0.29, 0.46, 0.69, and 0.79; propod posterior margin without spine group at 0.74. Peraeopod 5: propod posterior margin spined at 0.15 (2), 0.28 (4), 0.46 (4), 0.61 (3), 0.78 (3), and 0.93 (3).

Uropod 3: peduncle with a single long spine dorsally. Telson with 3 long and 1 short spines on each lobe.

Remarks

Waematau triregis can be easily recognised by the very distinctive male second gnathopod. Except for the secondary sexual characters there is little sexual dimorphism between the male and the female. Many of the differences which do occur between the types, in spination for example, can be accounted for by differential wear, since the range of variation seen in other specimens of the species is quite broad. But the broadening of certain peraeopod segments in the female does seem to be a true dimorphism.

Nothing is known of the ecology of this species. In particular, it would be interesting to know if it does occur in kauri (Agathis australis) litter. It has been recorded as occuring in kauri reserves, but these are usually composite mosaics of two very distinctive communities: one dominated by kauri, and the other by taraire (Beilschmiedia tarairi) (Cockayne, 1908). I have shown in Part II of this work that kauri litter contains substances which are toxic to Makawe hurleyi. W.triregis may have specific protective mechanisms which permit survival in kauri litter, but I have never collected it there so it is more probable that, although it lives near kauri, it is actually in the taraire litter community. In extensive trials I extracted very few animals of any kind from kauri litter: only a few nematodes, and ciliates, and no meso- or macrofauna; certainly, no amphipods were present.

However, even taraire litter would, on first sight, be a stressful environment for talitrids since Ca^{++} levels are low and the soils are very acid, and this would mitigate against organisms which make such great use of calcium as do talitrids. Perhaps they have specific ion conservation mechanisms which enable them to thrive in such apparently unsuitable environments.

Waematau reinga new species

Figures 241 to 254.

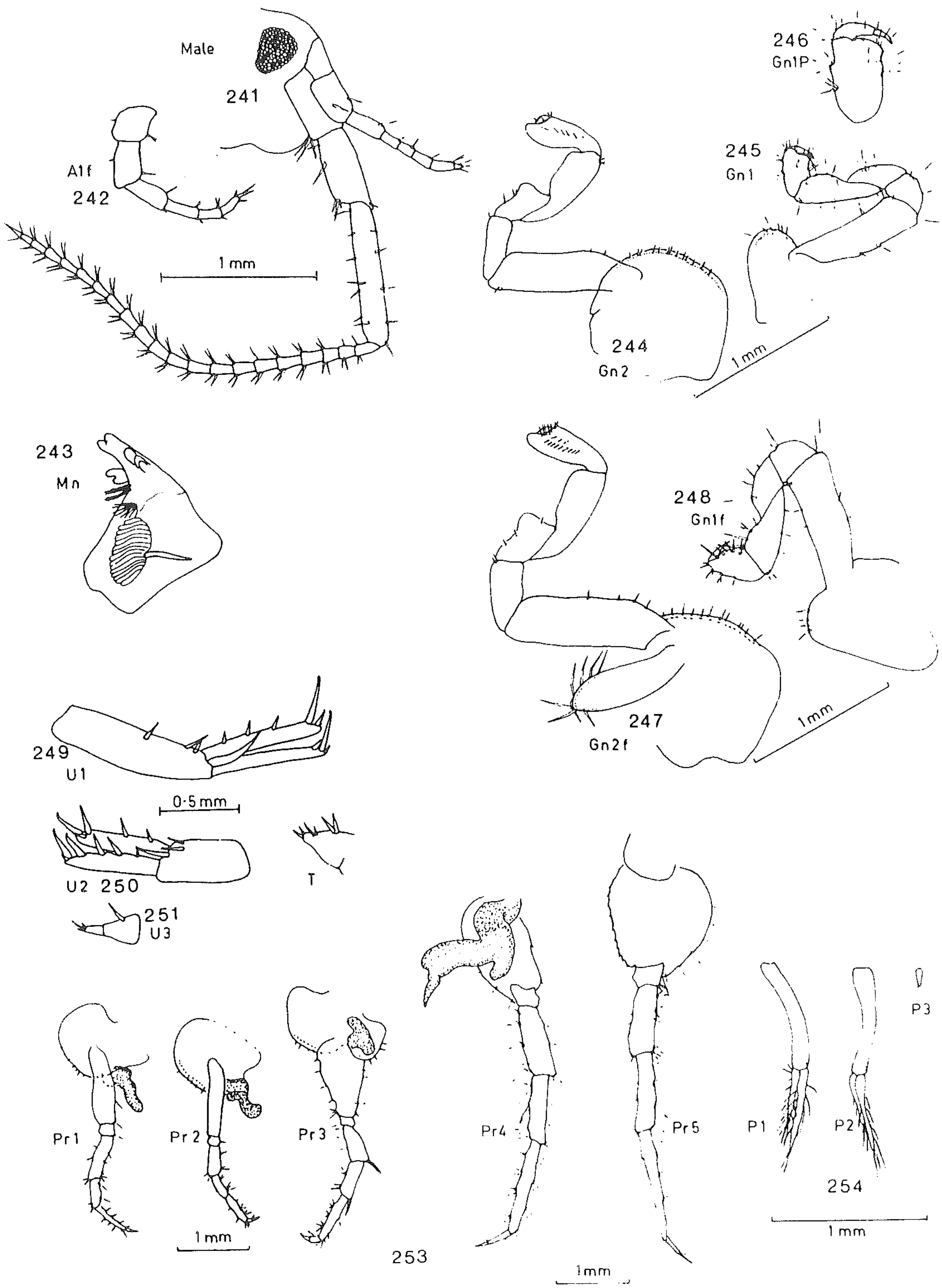
Types:

The holotype male and allotype female were collected at East Spirits Bay, Unuwhao, on 29/XI/1960, by B.Holloway, and have been deposited in the Canterbury Museum. Author's Catalogue No. KD 633).

Diagnosis:

A moderate sized, weakly sexually dimorphic landhopper of the genus Waematau with a short antenna 1 which extends to 0.2 along the last segment of the antenna 2 peduncle; antenna 2 with about 22 podomeres each with a few, long spines, eye ellipsoid and not very dark; mandible lacinia mobilis small, gnathopod 1 chelate in both sexes, with a long finger which protrudes beyond propod margin, a plinthic ridge is absent, gnathopod 2 propod is mitten-shaped in both sexes, peraeopods somewhat short and peg-like, the margins of the coxal plates have many small spines; the gills are large with the last pair having a long pointed pendulous lobe, broodplates sparsely setose, the first and second pleopods are long and biramous, though sparsely setose, with 2 coupling spines; third pleopod reduced to a vestigial stump; uropod 1 peduncle weakly spined; outer ramus naked, with a very long inter-ramal spur which extends 0.5 along rami, uropod 2 both rami spined, telson slightly cleft with about 7 marginal spines.

Description



FIGURES 241-254. Waematau reinga. 241, cephalon. 242, antenna 1 female. 243, mandible. 244, gnathopod 2 male. 245, gnathopod 1 male. 246, gnathopod 1 male propod. 247, gnathopod 2 female. 248, gnathopod 1 female. 249, uropod 1. 250, uropod 2. 251, uropod 3. 252, telson. 253, peraeopods 1,2,3,4 & 5. 254, pleopods 1,2 &3.

Male:

Length 12.2 mm; Eye not very dark, ellipsoid in outline. Antenna 1: length 1.28 mm, peduncle segment 1 margins convex, superodistal angle with 2 spines; segment 2 margins subparallel, superodistal angle with 2 spines, posterodistal angle with 1 spine; segment 3 narrower than segment 2, distal angles with 2 spines each; peduncle of 5 podomere segments, first the longest, podomere segments 1 and 2 have long spines at superodistal angle and 2 small spines at inferodistal angles; podomere segment three has long spines at superodistal and inferodistal angles; podomere segment 4 has 1 dorsal spine; podomere segment 5 is short and triangular with a short, close-bound terminal tuft. Antenna 2: length 4.51 mm; peduncle segment 3 broadening distally, with a prominent patch of 3 long spines at inferodistal angle; segment 4 superior margin naked, superodistal angle with 1 small spine, inferior margin with 4 spines, inferodistal angle with 4 longer spines; segment 5 long and narrow, spines are long and delicate; peduncle of 21 podomere segments, long and tapering, each podomere segment is longer than broad with concave margins, and 2 long spines in each of the 4 distal angles; last segment is long and conical with a tight tuft of terminal setae.

Mouthparts: Upper lip: ventral margin rounded, setose. Maxilla: mandible 4-toothed, a flat plate like saw shape, lacinia mobilis, small, 4-toothed; 2 intermediate pilose setae present, setal tuft prominent, molar 17-striate, molar medial seta present, about twice molar width. Lower lip: ventral margin rounded, sparsely setose. Maxilliped: palps comparatively broad, segment 4 not obscured; inner plate teeth very large.

Gnathopod 1: coxal plate short, ventral margin straight, with about 6 spines, no plinthic ridge present; basos broadening distally, anterior margin slightly concave, spined at 0.70, 0.92, and 0.96, posterior margin convex and stepped, spined at 0.57, posterodistal angle with 2 large spines; ischium comparatively large, anterior margin not produced, posterior margin convex, spined at 0.50, posterodistal angle with 1 large and 1 small spine; merus posterior margin scarcely produced, convex, with large spines at 0.22, 0.42, 0.55, 0.62, and 0.67; carpus anterior margin nearly straight, spined at 0.27, 0.57, and 0.69, anterodistal angle with 3 spines, posterior margin convex, stepped, not produced to a pellucid lobe, spined at 0.20, 0.31, 0.51, 0.62, and 0.76; propod broadening distally, anterior margin stepped, spined at 0.35, 0.58, and 0.85, anterodistal angle with 2 long spines, posterior margin spined at 0.52 and 0.72, palm extends to edge of propod, flanked by long spines especially posteriorly, palm convex, palmar angle 108°; dactyl longer than palm, projects beyond propod posterior margin.

Gnathopod 2: coxal plate ventral margin rounded with many spines, many of which occur in pairs; basos anterior margin emarginate anteriorly, spined at 0.28 and 0.39, posterior margin slightly sinuous, naked, posterodistal angle with 1 small spine; ischium long, posterodistal angle with 1 spine; merus posterior margin produced to a pellucid lobe guarded by 3 or more spines at its base; carpus anterior margin long, anterodistal angle with 3 spines, posterior margin produced to a pellucid lobe; propod mitten-shaped, anterior margin naked, anterodistal angle with 2 spines, posterior margin produced into a pellucid lobe which projects well beyond the palmar area, palm short, oblique, palmar angle about 68°, a longitudinal row of spines runs to base of palm; dactyl short, occludes propod lobe.

Peraeopod 1: coxal plate ventral margin nearly straight, with 12 spines; basos broadening distally, anterior margin convex, posterior margin slightly stepped, spined at 0.30, 0.49, and 0.72; ischium posterodistal angle with 2 spines; merus anterior margin spined at 0.29 and 0.58, anterodistal angle with 2 spines, posterior margin spined at 0.16, 0.26, and 0.53, posterodistal angle with 3 spines; carpus narrows distally, anterior margin convex, naked, posterior margin slightly emarginated proximally, spined at 0.23, 0.51, and 0.74; propod scalloped, curved posteriorly, anterior margin spined at 0.18 (1), 0.41 (2), 0.61 (2), and 0.80 (2), anterodistal angle with 1 spine, posterior margin spined at 0.29 (3), 0.51 (3), and 0.74 (3), posterodistal angle with 3 spines; dactyl long and conical, with 1 small spine on anterior margin and 1 larger on posterior margin at base of terminal spine.

Peraeopod 2: coxal plate ventral margin nearly straight with 11 small spines, anterior angle rounded; gill discoidal with partly rolled edges; basos to merus not clear in type; carpus anterior margin with 1 small spine at 0.47, posterior margin spined at 0.18 (3), and 0.68 (3); propod margins stepped, narrowing slightly distally, anterior margin spined at 0.35 (2), and 0.75 (2), posterior margin spined at 0.26 (2), 0.49 (2), and 0.75 (3); dactyl long, conical.

Peraeopod 3: coxal plate lobes less produced than usual, each lobe has about 4 spines; gill small, discoidal; basos broad proximally, narrowing distally, anterior margin with large spines at 0.12, 0.28, 0.59 and 0.77, posterior margin spined at 0.28, 0.42, 0.72, 0.81, 0.87, and 0.97; ischium anterodistal angle with 1 very large spine; merus very broad distally, anterior margin slightly scalloped, with large spines at 0.21, 0.33, 0.48, and 0.73, anterodistal angle with 4 large spines, posterior margin with 1 small spine at 0.48, posterodistal angle with 1 very long and 1 minute spine; carpus narrower than merus but as long, anterior margin with long spines at 0.11 (1), 0.36 (3), 0.71 (1), and 0.79 (1), posterior margin naked, posterodistal angle with 3 large spines; propod narrowing distally, anterior margin scalloped and stepped, spined at 0.18 (1), 0.30 (2), 0.54 (2), and 0.82 (3), posterior margin stepped, spined at 0.46 (1+1), and 0.83 (1+1), posterodistal angle with 3 spines; dactyl not curved, conical, terminal spine curved anteriorly.

Peraeopod 4: coxal plate small, ventral margin rounded with a few minute spines; gill large, trilobed, pendulous lobe narrow, tapering, terminates distally acutely; basos longer than broad, anterior margin rounded with 9 larger spines, posterior margin with 8 smaller spines; ischium anterodistal angle with 1 spine; merus broadening distally, anterior margin scalloped, spined at 0.15 (1), 0.31 (2), 0.59 (2), and 0.84 (1), anterodistal angle with 2 spines, posterior margin stepped, with smaller spines at 0.37, and 0.60, posterodistal angle with 2 large spines; carpus margins subparallel, anterior margin scalloped, spined at 0.08 (1), 0.21 (3), 0.48 (3), 0.82 (1), and 0.87 (4), posterior margin straight, with minute spines at 0.39, and 0.67, posterodistal angle with 3 large spines; propod both margins stepped and somewhat scalloped, anterior margin spined at 0.17 (2), 0.36 (3), 0.55 (3), and 0.84 (3), posterior margin spined at 0.19 (1), 0.42 (2), 0.70 (3), and 0.95 (3), posterodistal angle with 1 spine; dactyl long, narrow, tapering, terminal spine only slightly curved anteriorly.

Peraeopod 5: coxal plate margins rounded, naked; basos as broad as long, an inverted pear-shape, anterior margin smoothly convex with large spines, posterior margin minutely scalloped with minute spines; ischium anterodistal angle with 3 spines; merus broadening slightly distally, anterior margin stepped, spined at 0.15 (1), 0.25 (2), 0.44 (3), 0.60 (1), and 0.73 (4), anterodistal angle with 4 large spines, posterior margin with small spines at 0.29, 0.42, 0.55, and 0.68, posterodistal angle with 1 spine; carpus margins subparallel, anterior margin scalloped, spined at 0.17 (1), 0.37 (2), 0.63 (2), anterodistal angle with 3 spines, posterior margin with minute spines at 0.37, and 0.63, posterodistal angle with 2 large spines; propod long, narrowing distally, anterior margin strongly stepped, spined at 0.12 (0+1), 0.25 (2), 0.41 (3), 0.64 (3), and 0.87 (3), anterodistal angle with 2 long spines, posterior margin weakly stepped, spined at 0.24 (2), 0.41 (2), 0.67 (2), and 0.92 (2), posterodistal angle with 1 spine; dactyl long and conical.

Pleopod 1: length 1.20 mm, narrow, delicate and biramous, peduncle slender, margins naked, 2 coupling spines present; rami weakly setose, outer ramus much shorter than inner.

Pleopod 2: length 1.13 mm, peduncle margins naked, 2 coupling spines present; rami sparsely setose, inner twice length outer. Third: reduced to a short, triangular stump with 1 minute spine on its tip.

Uropod 1: only few spines scionate with long, very fine scions which extend well beyond spine tip; peduncle with 3 dorsal spines at 0.56, 0.84, and 0.90, inter-ramal spur large, 0.5 length of rami; rami long, outer ramus naked, terminates with 1 very long and 2 short spines; inner ramus with 3 dorsal spines at 0.18, 0.40, and 0.60, terminates with 1 very long and 1 shorter spine. Uropod 2: peduncle with 2 dorsal spines and 1 long inter-ramal spine; both rami spined dorsally; terminate in 2 long and 2 shorter spines. Telson: slightly cleft, margins with 3 pairs of spines.

Female: as for male except where noted.

Antenna 1: broader than male; peduncle segment 1 with 2 spines at superodistal angle, 1 spine midway on inferior margin; segment 2 with 1 small spine on mid-inferior margin. Antenna 2: length 5.06 mm; Mouthparts: Maxilla 1: outer plate with a small palp, distal margin with 9 spine teeth with 0, 0, 1, 4, 4, 4, 2, 4, 1 lateral teeth; inner plate terminal setae not very long. Maxilliped: inner plate distal margin with 2 large spine teeth, pilose setae arranged in a short diagonal row below this, which does not extend down the midline.

Gnathopod 1: basos anterior margin spined at 0.43, 0.56, 0.70, and 0.96, posterior margin spined at 0.40, and 0.58, posterodistal angle with 1 very long and 1 long spine.

Gnathopod 2: broodplate elongated, distal margin rounded with

8 spines; basos anterior margin spined at 0.12, 0.27, 0.37, and 0.57.

Peraeopod 1: broodplate distal margin comes to a rounded point, with about 8 setae; basos anterior margin spined at 0.48, 0.54, 0.69, 0.74, and 0.88, posterior margin spined at 0.49 and 0.52, posterodistal angle with 1 large spine; dactyl inner margin slightly emarginate.

Peraeopod 2: broodplate distal margin rounded, with 8 setae; basos slightly curved anteriorly, anterior margin spined at 0.57, 0.69, 0.79, and 0.90, posterior margin spined at 0.29, 0.47, and 0.68; ischium with 2 spines at posterodistal angle; merus broadening distally, anterior margin with 1 small spine at 0.40, anterodistal angle with 2 spines, posterior margin spined at 0.36 and 0.50, posterodistal angle with 3 large spines; dactyl inner margin markedly emarginate. Peraeopod 3: basos with 2 longer spines at posterodistal angle. Peraeopod 4: basos posterior margin more rounded, with 12 minute spines; ischium anterodistal angle with 2 spines; carpus anterior margin spined at 0.12 (1), 0.31 (3), 0.57 (3), 0.82 (3), 0.88 (2), and 0.92 (1), posterior margin spined at 0.42 and 0.79, posterodistal angle with 1 spine; propod anterior margin spined at 0.14 (1), 0.23 (2), 0.40 (3), 0.62 (3), and 0.86 (3), posterior margin spined at 0.23 (2), 0.46 (3), and 0.75 (3), posterodistal angle with 4 spines.

Peraeopod 5: merus anterior margin spined at 0.13 (2), 0.35 (3), and 0.64 (3) anterodistal angle with 3 spines, posterior margin spined at 0.25, 0.40, and 0.62, posterodistal angle with 1 spine; propod anterior margin spined at 0.20 (2), 0.34 (2), 0.51 (3), 0.70

(3), and 0.90 (2), posterior margin spined at 0.20 (2), 0.34 (3), 0.53 (3), and 0.76 (3), posterodistal angle with 3 spines.

Uropod 1: inter-ramal spur extends beyond 0.5 length of rami; outer ramus naked, inner ramus with 2 dorsal spines, terminates in 1 long, scionate spine and 2 shorter spines. Uropod 3: peduncle with 1 spine, ramus with 1 longer and 2 shorter terminal spines.

Remarks

W. reinga is readily distinguished from any other known species by its pleopods and the extremely long inter-ramal spur on uropod 1. It would be interesting to know more about its distribution around the North Cape-Cape Reinga district since this area was once a volcanic island or seamount, and is now connected to Northland by a long sand spit which still effectively isolates these species from the very north of the North Island.

Waematau kaitaia new species

Figures 255 to 271

Types: The holotype male was collected from Mt Horokaka, Tangihua, Kaitaia at 518 m, by J.S.Dugdale, on 16/VIII/1977, ex litter 77/79, and has been deposited in the Canterbury Museum. (Author's catalogue no. KD 904). The paratype male from same locality has been deposited in the National Museum. The above two specimens were taken together with *Tara sylvicola*.

Etymology. The specific epithet is derived from the type locality.

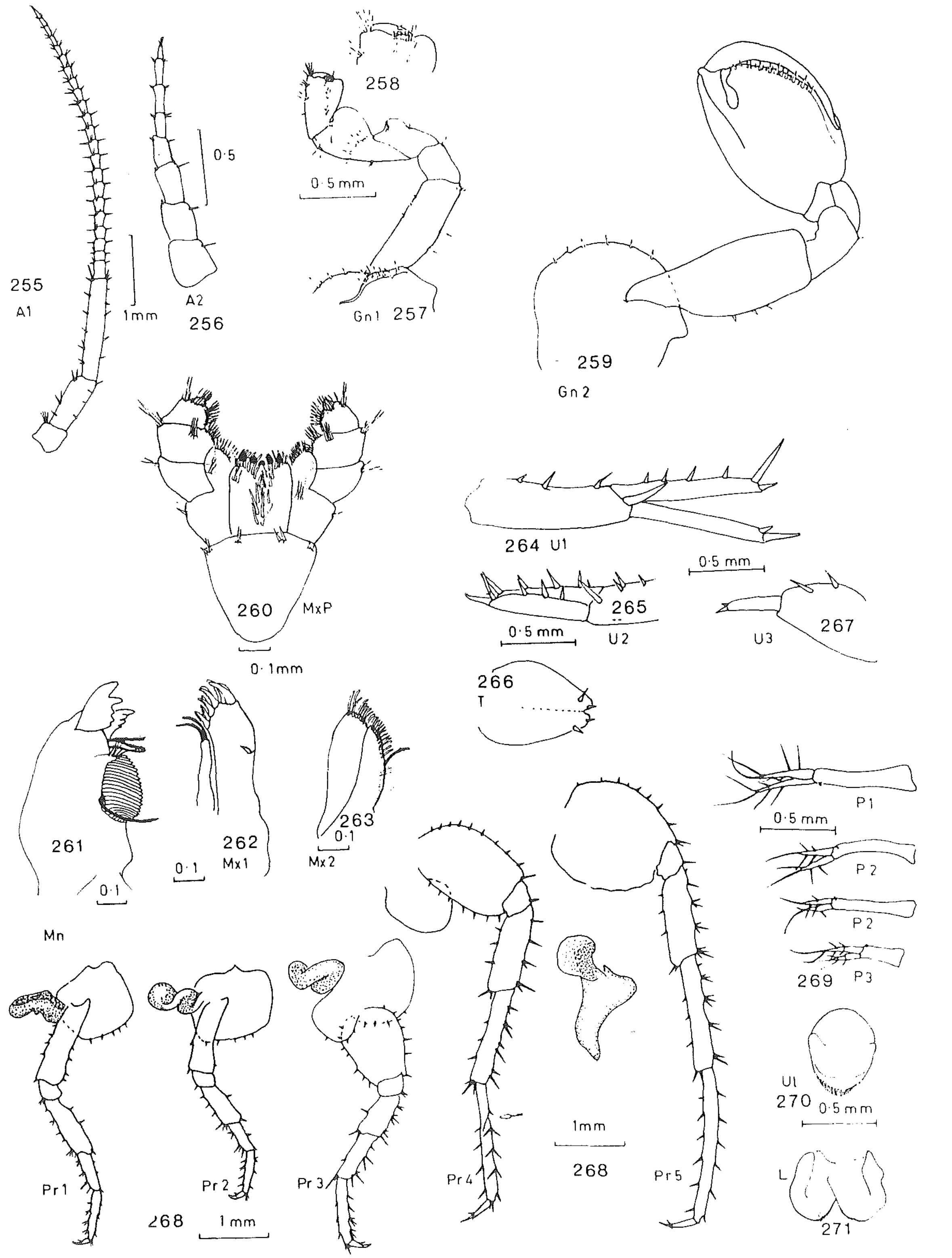
Diagnosis:

A large landhopper, of the genus *Waematau*, with long, slender antenna 2, antenna 1 extends to 0.25 along antenna 2 peduncle segment 5; gnathopod 1 male chelate; gnathopod 2 male propod expanded, ellipsoid with a long convex palm, dactyl curved, longer than palm, with a soft tip; gills large and spirally rolled; uropod 1 outer ramus naked; uropod 2 both rami spined, equal in length; uropod 3 and telson are flattened plates which act as faecal guides; pleopods all present but reduced, particularly the third.

Description:

Male:

Length 13.5 mm, width 2.39 mm, depth 2.40 mm. Body shallow. Pigmentation in alcohol of banded type with 2 pink-red hoops per



FIGURES 255–271. Waematau kaitaia. 255, uropod 2. 256, uropod 1. 257, gnathopod 1. 258, gnathopod 1 palm. 259, gnathopod 2. 260, maxilliped. 261, mandible. 262, maxilla 1. 263, maxilla 2. 264, uropod 1. 265, uropod 2. 266, uropod 3. 267, telson. 268, peraeopods 1,2,3,4 & 5. 269, pleopods 1,2 & 3. 270, upper lip. 271, lower lip.

abdominal segment which merge dorsally to form a diffuse longitudinal stripe mid-dorsally. Antenna 1: length 1.68 mm; peduncle segments all about same length; segment 1 narrowing distally, spined at superodistal angle; segment 2 narrower, both superior and inferior margins convex, spined at superodistal and inferodistal angles; segment 3 margins nearly straight, broadening distally, superodistal and inferodistal angles each with 2-3 spines; flagellum of 5 podomere segments tapering distally, each segment except last with 3 spines at distal angles; first podomere is recurved superiorly so that flagellum is inclined upwards and away from antenna 2.

Antenna 2: length 6.74 mm; comparatively long, fine and tapering; peduncle segment 3 inferodistal angle with a patch of spines; segment 4, 2.2 times length of segment 3 , broadening distally to be as nearly as broad distally as segment 3, superior margin straight, with 3 spines, superodistal angle with 1 spine, inferior margin with larger spines at 0.17 (1), and 0.36 (2), inferodistal angle with 3 spines; segment 5, 1.8 times length of segment 4, but narrower, superior margin spined at 0.22, 0.39, 0.50, 0.61, 0.73, and 0.85, superodistal angle with 4 spines, inferior margin with pairs of spines at 0.14, 0.28, 0.46, 0.64, 0.82, and 0.98, inferodistal angle with 2 spines; flagellum length 4.08 mm, with 22 podomere segments; each podomere segment spined at each of the distal angles with 3 setae; terminal tuft sparse, short.

Mouthparts: Upper lip: more ovate than usual, distal margin strongly setose, inner shelf present. Mandible: incisor large, 5-cuspate, with a characteristic saw-toothed linear shape, lacinia mobilis 4-toothed, 4 interdentate pilose setae on inner margin, setal tuft proximal to these on distal margin of molar prominence; molar about 24-striate, molar medial seta prominent and pilose. Lower lip setose distally on inner margins only, frontal setal row short, sparse. Maxilla 1: inner plate narrowing distally, terminates in 2 long pilose setae; outer plate margins subparallel, oblique distal margin with 9 teeth, outer margin bearing a minute palp. Maxilla 2: outer plate curved somewhat inwardly, distal margin with inwardly curved setae outer margin sparsely pilose; outer plate distal margin oblique, with inwardly curved setae terminating with a strong, pilose seta, inner margin pilose. Maxilliped: broad, inner plate distal margin rounded with 2 large and 1 small spine teeth, pilose setae are set below these and down inner margins; outer plate with setal row on rounded distal margins; basal segment 1 with 2-3 spines at outer distal angles, and 2 spines at 2 groups mesially on distal margin; segment 2 broader, with 1 spine at distal angles and 3 spines mesially; palp broad, heavily setose on inner margins; palp segment 4 present but nearly completely obscured by the distal spines on segment 3.

Gnathopod 1: coxal plate ventral margin rounded, with 5-6 large spines; plinthic ridge present as a thickened shelf with 7 large spines; basos broadening distally, anterior margin straight, with small spines at 0.59, 0.70, and 0.79, posterior margin convex, with larger spines at 0.33 and 0.53, posterodistal angle with 3 smaller spines; ischium anterior margin only slightly sinuous, posterior margin naked except for 2 larger spines at posterodistal angle; merus posterior margin broadening distally to a discrete pellucid lobe guarded by 3 larger spines at its base; carpus anterior margin convexly rounded, spined at 0.38 and 0.60 and at anterodistal angle (3), the whole posterior margin is produced to a pellucid lobe guarded by a proximal row of 5 large spines running almost transversely and another transverse row of 4 large spines distally; propod broadening distally, anterior margin convex, spined at 0.38 (1), 0.62 (2), and 0.83 (3), posterodistal angle with a tight group of 6 spines, posterior margin produced to a pellucid lobe, especially distally, which projects slightly beyond palm, protected by about 5 large spines on each face, palm short, slightly convex, flanked by a row of 5 spines on each side, these spines grow larger posteriorly, palmar angle 90°; dactyl short, about 0.66 propod width, inner margin with 2 spines, distal margin at base of terminal spine with 3 spines, distal tip curved inwards so occluding pellucid lobe.

Gnathopod 2: coxal plate ventral margin rounded, with 6 relatively large spines; basos broadest medially, anterior margin naked, very slightly sinuous, posterior margin convex, spined at 0.41, 0.55 and 0.66, posterodistal angle with 1 spine; ischium relatively long, broadest distally, posterodistal angle with 1 spine; merus and carpus short and triangular; propod greatly produced, strongly subchelate, ovate, anterior margin very slightly emarginate, palm long, convex, flanked by many short, stout spines, palmar angle 138°, a longitudinal ridge runs down the face to the anterior of the dactyl base; dactyl long, much longer than palm, curved inwardly, margins naked, terminates distally with a slightly recurved, 'soft' tip which sits on a shelf-like extension of the palm.

Peraeopod 1: coxal plate distal angle rounded, ventral margin convex, spined; gill relatively large, margins rolled so that whole forms a spiral; basos expanded slightly distally, curved only slightly anteriorly, anterior margin concave, spined at 0.56, 0.69, 0.86, and 0.94, posterior margin convex, stepped at spine bases, spined at 0.25, 0.39, 0.53 and 0.67, posterodistal angle with 1 spine; ischium with 2 spines at posterodistal angle; merus broadening distally, anterior margin convex, stepped at spine bases, spined at 0.24 and 0.48, anterodistal angle with 2 spines, posterior margins scalloped between spine bases, spined at 0.18 (2), 0.37 (2), 0.59 (2), 0.71 (1) and 0.91 (2+1), posterodistal angle with 2 spines; carpus anterior margin nearly straight, spined at 0.24 and 0.37, anterodistal angle with 1 spine, posterior margin scalloped between spine bases, spined at 0.23 (2), 0.52 (3), 0.77 (3) and 0.89 (2), propod narrowing distally, both margins stepped at spine bases, anterior margin spined at 0.24, 0.50, and 0.83, anterodistal angle with 3 spines, posterior margin spined at 0.25 (3), 0.43 (3), 0.64 (3) and 0.82 (4); dactyl inner margin slightly emarginated.

Peraeopod 2: coxal plate subsquare, distal angles rounded, ventral margin straight, with 6 spines; gill a discoid twisted into a spiral; basos broadening slightly distally, curved only slightly anteriorly, anterior margin concave, spined at 0.61 and 0.86 (2), posterior margin spined at 0.31 and 0.67, posterodistal angle with 1 spine; ischium posterodistal angle with 1 spine; merus broadening distally, anterior margin spined and stepped at 0.37, anterodistal angle with 2 spines, posterior margin nearly straight and only slightly stepped, spined at 0.23 (2), 0.45 (2), and 0.67 (1), posterodistal angle with 3 spines; carpus short and narrow, anterior margin spined at 0.30, anterodistal angle with 1 spine, posterior margin scalloped between spines, spined at 0.32 (2), and 0.68 (2+2); propod narrowing slightly distally, anterior margin convex, stepped, spined at 0.18, 0.46, and 0.79, anterodistal angle with 3 spines, posterior margin stepped, spined at 0.28 (1+1), 0.45 (3), 0.66 (3), and 0.84 (4); dactyl inner margin scarcely emarginate.

Peraeopod 3: coxal plate bilobed, anterior lobe with 3 marginal spines, posterior lobe with 4 spines; gill discoidal twisted into a spiral; basos broadest proximally, an inverted pyriform shape, anterior margin with 6 larger spines, anterodistal angle with 3 spines, posterior margin with 9 spines; ischium anterodistal angle with 4 spines; merus broadening distally, anterior margin scalloped, spined at 0.25 (3), 0.49 (3), and 0.89 (3), anterodistal angle with 1 spine, posterior margin convex, (with a minute spine at 0.24 and a larger one at 0.53), posterodistal angle with 3 spines; carpus margins subparallel, anterior margin scalloped, spined at 0.21 (2), 0.42 (2), 0.51 (1), 0.78 (2), and 0.90 (1), posterior margin straight, spined at 0.60, posterodistal angle with 3 spines; propod tapering slightly distally, both margins stepped, anterior margin spined at 0.27 (2), 0.44 (3), 0.64 (3), and 0.84 (3), posterior margin spined at 0.38, 0.57, and 0.83, posterodistal angle with 3 spines; dactyl long, slightly curved.

Peraeopod 4: coxal plate rounded; basos ellipsoid, anterior margin with 10 large spines, anterodistal angle with 2 spines, posterior margin with 8 smaller spines; ischium anterodistal angle with 2 spines; merus broadening distally, both margins stepped, anterior margin spined at 0.09 (1), 0.21 (2), 0.41 (2), 0.68 (3), and 0.90 (2), anterodistal angle with 2 spines, posterior margin spined at 0.19 (1), 0.38 (1), and 0.63 (1+1), posterodistal angle with 3 spines; carpus narrow, broadening distally, anterior margin scalloped, spined at 0.20 (2), 0.38 (3), 0.61 (3), and 0.88 (2), posterior margin stepped, spined at 0.36, 0.55, and 0.77, posterodistal angle with 4 large spines; propod long and narrow (damaged in mounted type) , anterior margin slightly scalloped, spined at 0.11 (1), 0.23 (2), 0.37 (2), 0.54 (2), 0.72 (2), and 0.93 (2), anterodistal angle with 2 spines, posterior margin spined at 0.27 (2), 0.36 (2), 0.50 (2), 0.79 (1), and 0.90 (2); dactyl long and conical, base curved slightly anteriorly.

Peraeopod 5: gill not very large, pendulous lobe triangular; basos broad, anterior margin smoothly convex, with 9 large spines, anterodistal angle with 3 spines, posterior margin scalloped with about 7 minute spines; ischium anterior margin straight, anterodistal angle with 2 large spines; merus broadening distally, anterior margin scalloped, spined at 0.09 (2), 0.21 (3), 0.42 (3), 0.66 (3), and 0.94 (5), posterior margin only slightly stepped, spined at 0.17, 0.34, and 0.60, posterodistal angle with 2 spines; carpus margins subparallel, anterior margin scalloped, spined at 0.10 (2), 0.19 (3), 0.38 (3), 0.63 (2), and 0.90 (3), posterior margin only slightly stepped and concave, spined at 0.30, 0.48, and 0.71, posterodistal angle with 3 spines; propod long, tapering distally, curved posteriorly, anterior margin stepped, spined at

0.16 (3), 0.31 (3), 0.46 (3), 0.61 (3), 0.77 (2), and 0.94 (2), anterodistal angle with 4 spines, posterior margin slightly stepped, spined at 0.11 (1), 0.18 (1), 0.31 (1), 0.44 (1), 0.59 (2), 0.76 (2), and 0.93 (2); dactyl long and conical, margins naked, anterodistal angle with 1 minute spine, posterodistal angle with 1 larger spine. Penal organ rectangular, nearly extends to midline.

Pleopods: all present, reduced, especially the second and third. Pleopod 1: biramous, with a pair of coupling spines, peduncle margins naked, rami short, sparsely setose, segmentation not obvious, inner ramus longer than outer; pleopod 2 and 3: biramous with only 1 coupling spine on inner margin; rami very short, equal in length, sparsely setose, only about 3 segmented although segmentation difficult to determine; pleopod 2 shorter than pleopod 1; pleopod 3 very short.

Epimeral plates: First: triangular, posterodistal angle acute but not notched, posterior margin naked. Second subsquare, ventral margin somewhat rounded, posterior margin emarginated slightly above acute posterodistal angle, with only 1 minute spine. Third: anterodistal angle rounded, posterodistal angle acute, ventral margin rounded, posterior margin emarginated ('notched') distally, with 1 minute spine proximally.

Uropod 1: peduncle with 3 spines dorsally, inter-ramal spur about 0.33 ramus length; outer ramus naked dorsally, terminates in 1 long and 2 short spines; inner ramus with 4 spines dorsally, terminates with 1 long and 1 short spine, terminal spines on each ramus with a slight distal hook. Uropod 2: peduncle with 3 dorsal spines, inter-ramal spur present; both rami spined dorsally.

Uropod 3: uniramous; peduncle forms a flat faecal guide, with 2 stout marginal spines; ramus naked except for 2 short terminal spines. Telson: only slightly cleft, with 2 marginal spines on each lobe.

Remarks

The female has not been identified with certainty because it occurs with many other species and is hard to separate from the females of these other species in the limited collections available. In view of the environmental modification that is taking place in Northland it is a matter of some urgency that extensive collections be made of this and the other species that occur in this faunistically rich province. Certainly, such a collection would establish just how much a threat Talitroides topitotum is to the native species.

Waematau kaitaia is distinguished from Parorchestia tenuis, and other similar species, by its double hooped pigmentation pattern, its long antenna 2, the characteristic gnathopods, the reduced but biramous pleopods, the naked outer ramus of uropod 1, and the spined rami on uropod 2. It can be distinguished from W.unuwhao, which it closely resembles, by the following characters: longer, more tapering antenna 2, and pleopods all present and biramous (though these are fine with the third quite small). Its naked outer ramus of uropod 1 distinguishes it from Tara sylvicola.

Waematau unuwhao new species

Figures 272 to 300

Types:

The holotype and allotype female were collected from a forest remnant, at 183 m altitude, 5 km SE of Unuwhao in the North Cape area, Northland, on 24/XI/1967, by K.A.J.Wise, and have been deposited in the Canterbury Museum (slide plus tube containing dissected remains) (Author's catalogue no. KD 894).

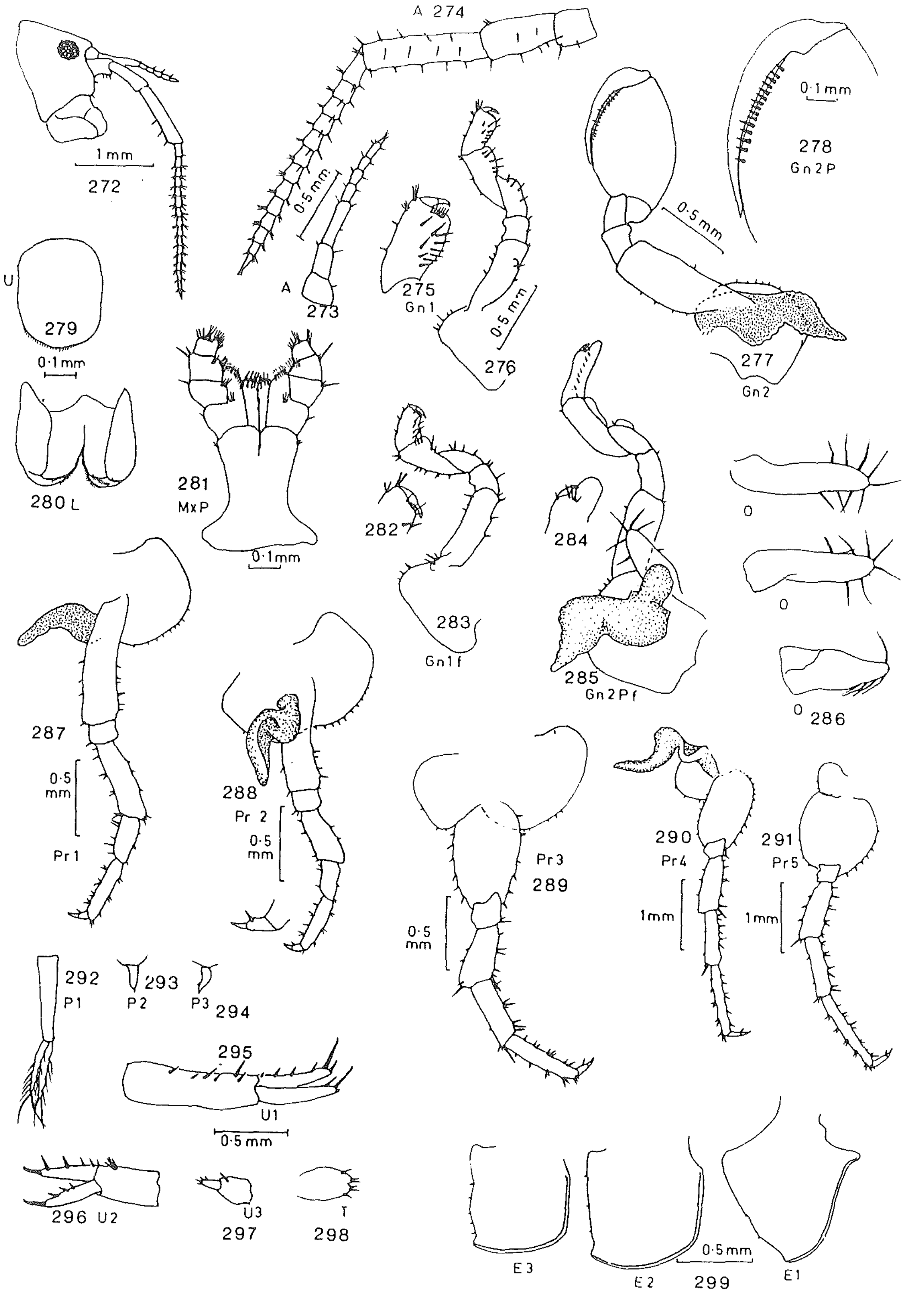
Etymology. The specific epithet is derived from the type locality.

Localities:

The only known locality in which this species occurs is the type locality where it was collected by K.A.J.Wise together with *Waematau espiratus* and *Parorchestia tenuis*.

Diagnosis:

A small landhopper, of the genus *Waematau*, sexually dimorphic, body not very deep, eyes dark, round; antenna 1 extends to between 0.33 and 0.5 along antenna 2 peduncle segment 5, antenna 2 short, gnathopod 1 chelate in both sexes, male gnathopod 2 propod ovate with a long, oblique, convexly curved palm and a long overlapping dactyl with a soft tip, female gnathopod 2 mitten-shaped,peraeopods relatively short and stout; pleopod 1 small but biramous, pleopod 2 reduced to a cylindrical vestige, pleopod 3 even more reduced to a triangular stump, uropod 1 outer ramus naked, inner ramus weakly



FIGURES 272-299. Waematau unuwhao. 272, cephalon. 273, antenna 1. 274, antenna 2. 275, gnathopod 1 male propod. 276, gnathopod 1 male. 277, gnathopod 2 male. 278, gnathopod 2 male propod. 279, upper lip. 280, lower lip. 281, maxilliped. 282, gnathopod 1 female propod. 283, gnathopod 1 female. 284, gnathopod 2 female propod. 285, gnathopod 2 female. 286, oostegites. 287, peraeopod 1. 288, peraeopod 2. 289, peraeopod 3. 290, peraeopod 4. 291, peraeopod 5. 292, pleopod 1. 293, pleopod 2. 294, pleopod 3. 295, uropod 1. 296, uropod 2. 297, uropod 3. 298, telson. 299, epimeral plates 1,2 & 3.

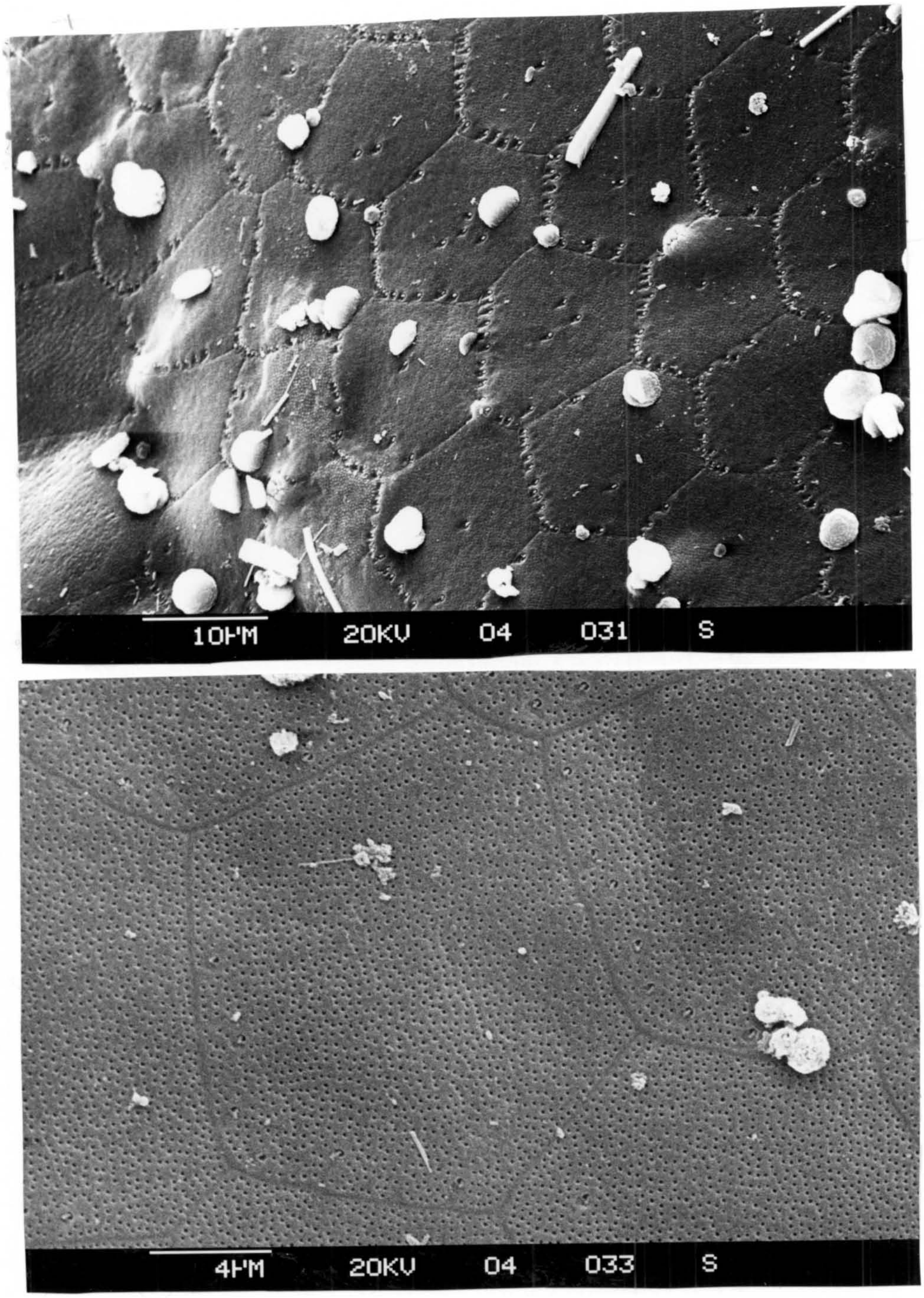


FIGURE 300. Cuticular structures of Waematau unuwhao. The upper micrograph is of the dorsal surface of thoracic segment 2 and shows well defined cuticular polygons, mesopores scattered over the surface as well as arranged in arcs on the posterior margins of the polygons, the latter mesopores open between ridges. The middle micrograph shows the midlateral of the same body segment; macropores are present not opening into dermal gland polygons, mesopores are scattered and arranged into arcs with overhanging 'verandas'. The lower micrograph is of the ventrolateral surface of the same body segment; here the polygons are very well defined, mesopore density is low but the mesopores are still arranged in arcs as well as being scattered over the surface.

spined, no inter-ramal spur; uropod 2 both rami spined, uropod 3 form broad plates or faecal guides, all uropods have very long, relatively straight terminal spines, telson forms a dorsal flat faecal guide, with long spines.

Description:

Male:

Length 8.59 mm, width 1.65 mm, depth 1.68 mm; eyes round, not very black, diameter 0.33 head length. Antenna 1: length 1.26 mm, extends to 0.33 to 0.5 along antenna 2 peduncle segment 5; peduncle segment 1 narrowing distally, with 1 spine at inferodistal angle; segment 2 slightly longer than segment 1 but narrower, with 1 small spine at superodistal angle and a larger one at the inferodistal angle; segment 3, 1.5 length of segment 2, superodistal angle with 1 spine, inferior margin with 1 spine midway and 2 spines at distal angle; flagellum has 5 podomere segments, first and fourth podomere segments the longest; flagellum not very tapering; each podomere is spined at supero- and inferodistal angles; ultimate podomere short and conical with a loose-bound and sparse terminal setal tuft.

Antenna 2: length 3.23 mm; peduncle segment 3 widening a little distally, spined at midinferior margin and at inferodistal angle (2); segment 4 superior margin naked except for 2 spines at superodistal angle, 2 spines midlateral, inferior margin slightly scalloped with 3 spines, inferodistal angle with 2 spines; segment 5, 1.6 segment 4 length but only 0.75 its width, superior margin has 4 spines, superodistal angle with 1 spine, lateral face has 5 spines, midlateral distal margin has 2 spines, inferior margin has 4 spines, inferodistal angle with 2 spines; flagellum of 13 podomere segments, each except for the last is finely setose at each of the four distal angles, last segment finely tapering with a short, close-bound terminal tuft.

Mouthparts: Upper lip: ventral margin rounded, only finely setose, no inner shelf. Mandible: incisor 5-cuspate, lacinia mobilis 4-cuspate; 2 pairs of interdentate pilose setae, between these and molar is a dense setal tuft, molar 18 striate, molar medial setae present and setose. Lower lip: setae confined to inner margin and inner region of distal margin. Maxilla 1: inner plate slender, terminating in two long, pilose setae; outer plate broader, margins subparallel, distal margin with 10 stout teeth, small palp present. Maxilla 2: outer plate outer margin convex, distal margin spined, inner plate subtriangular, distal margin spined, spine row terminates on inner margin with a long pilose seta. Maxilliped: not very broad, but palps broad, palp segment 4 small and almost masked by the spines on segment 3 and the produced inner distal margin of segment 3.

Gnathopod 1: coxal plate ventral margin somewhat stepped at spine groups, with 5 spines; basos curved slightly anteriorly, anterior margin slightly sinuous, spined at 0.46, 0.59, 0.69, 0.79, and 0.96, posterior margin convex, spined at 0.43 and 0.68, posterodistal angle with 1 spine; ischium posterior margin with one spine at 0.5, posterodistal angle with 2 spines; merus posterior margin produced to a pellucid lobe, with 4 spines; carpus broadening distally, anterior margin spined at 0.26, 0.35, and 0.63, posterior margin produced to a pellucid lobe distally and protected by 5 large spines around its base; propod shorter than carpus, anterior margin slightly stepped at spine groups, spined at 0.42 (2), 0.67 (1), and 0.89 (2), anterodistal angle with 4 spines, posterior margin slightly produced, palm short, flanked by a short row of about 6 spines, palmar angle 90°; dactyl shorter than propod width.

Gnathopod 2: coxal plate ventral margin rounded, with 9 spines; gill relatively small, bilobed; basos broadening distally, anterior margin sinuous, spined only at 0.53, posterior margin convex, spined at 0.24, 0.36, 0.54, and 0.68; ischium anterior margin produced, posterior margin slightly sinuous, posterodistal angle with 1 spine; merus short, posterior margin with 1 spine; carpus sort, triangular, margin convex; propod greatly produced, ellipsoid, palm long, oblique, convex, flanked by a row of short, stout spines on each side, palmar angle 26°, posterior end with recess to receive dactyl tip; dactyl long, longer than palm, with curved 'soft tip' bearing a small accessory sensory spine.

Peraeopod 1: coxal plate ventral margin rounded, with 11 spines; gill small, discoidal, basos broadening distally, curved anteriorly, anterior margin concave, spined at 0.57, 0.64, 0.70, 0.80, 0.88, and 0.96, posterior margin convex, spined at 0.45 (1), 0.59 (1), and 0.74 (2), posterodistal angle with 1 spine; ischium anterior margin sinuous, posterior margin straight, posterodistal angle with 1 spine; merus broadening distally, anterior margin convex, somewhat stepped at spine groups, spined at 0.41 and 0.65, anterodistal angle with 3 spines, posterior margin sinuous, spined at 0.06 (1), 0.20 (2), 0.41 (1), 0.45 (2), 0.67 (1), 0.71 (2), and

0.89 (2), posterodistal angle with 2 spines; carpus short, narrowing distally, anterior margin spined at 0.25 (1) and 0.55 (2), anterodistal angle with 1 spine, posterior margin spined at 0.03, 0.28, 0.56, 0.72, and 0.87, posterodistal angle with 3 spines; propod curved a little posteriorly, margins somewhat stepped at spine groups, anterior margin spined at 0.23 (2), 0.54 (2), and 0.81 (2), anterodistal angle with 3 spines, posterior margin spined at 0.21 (2), 0.30 (3), 0.47 (3), 0.66 (3), 0.84 (3), and 0.91 (1).

Peraeopod 2: coxal plate rounded anteriorly, ventral margin with 11 spines, emarginated posteriorly, posterior margin rounded; gill discoidal; basos curved anteriorly, margins a little stepped at spine groups, anterior margin spined at 0.65, 0.72, 0.82, and 0.91, posterior margin spined at 0.65, 0.72, 0.82, and 0.91, posterior margin spined at 0.46 (2) and 0.69 (2), posterodistal angle with 1 spine; ischium anterior margin slightly produced and sinuous, posterodistal angle with 2 spines; merus broadening distally, anterior margin convex, spined at 0.35, 0.58, 0.93, and 0.95, posterior margin straight, spined at 0.10, 0.25, 0.47, 0.63, 0.86, and 0.90, posterodistal angle with 2 spines; carpus short, margins subparallel, slightly scalloped at spine groups, anterior margin spined at 0.47, anterodistal angle with 2 spines, posterior margin spined at 0.19 (2), 0.39 (2), and 0.83 (2), posterodistal angle with 1 spine, propod narrowing slightly distally, curved a little posteriorly, margins stepped at spine groups, anterior margin spined at 0.19 (3), 0.54 (3), and 0.82 (3), anterodistal angle with 3 spines, posterior margin spined at 0.21 (3), 0.40 (3), 0.60 (3), and 0.81 (3), posterodistal angle with 1 spine; dactyl inner (posterior) margin emarginate proximal to base of terminal spine.

Peraeopod 3: coxal plate, both lobes spined; gill small, discoidal; basos an inverted pear shape, narrowing distally, anterior margin with larger spines than posterior; ischium anterior margin straight, anterodistal angle spined, posterior margin a little produced; merus broadening distally, anterior margin somewhat scalloped, spined at 0.19, 0.43, 0.47, 0.77, and 0.90 (2), posterior margin spined at 0.42 and 0.60, posterodistal angle with 2 spines; carpus narrowing only slightly distally, anterior margin stepped at spine groups, spined at 0.19 (2), 0.50 (3), and 0.83 (2), anterodistal angle with 2 spines, posterior margin with small spines at 0.42 and 0.68, posterodistal angle with 2+2 spines; propod narrowing only slightly distally, broadest medially, anterior margin stepped, spined at 0.20 (2), 0.33 (3), 0.54 (3), and 0.77 (3), posterior margin also stepped, spined at 0.15 (1), 0.35 (3), 0.62 (3), and 0.86 (3), posterodistal angle with 4 spines; dactyl only slightly curved inwardly.

Peraeopod 4: coxal plate rounded, with a few very small spines ventrally; gill bilobed, pendulous lobe narrow and long; basos a characteristic ellipsoid shape with the anterior margin convex and with a number of spines, posterior margin, with a slight sinuosity due to shallow excavation proximally, has numerous small spines; ischium anterodistal angle with 2 spines, posterior margin slightly produced; merus broadening distally, anterior margin slightly stepped and spined at 0.10 (2), 0.23 (3), 0.45 (3), 0.71 (3), and 0.82 (1), anterodistal angle with 3 spines, posterior margin spined at 0.25 (1), 0.42 (1+1), and 0.66 (1+1), posterodistal angle with

1+1 spines; carpus margins subparallel, anterior margin scalloped, spined at 0.14 (3), 0.36 (3), 0.60 (3), and 0.81 (4), posterior margin straight, spined at 0.36 (2), 0.54 (2), and 0.72 (2), posterodistal angle with 3 spines; propod long, narrowing only slightly distally, both margins scalloped, anterior margin spined at 0.14 (2), 0.29 (2), 0.47 (2), 0.65 (3), 0.79 (1), and 0.89 (2), posterior margin spined at 0.20 (2), 0.33 (2), 0.51 (2), 0.72 (2), and 0.94 (2), posterodistal angle with 3 spines; dactyl long and conical, only terminal spine is curved inwardly.

Peraeopod 5: basos both margins convex and stepped at spine groups, anterior margin has the larger spines; ischium anterior margin straight, anterodistal angle with 1 spine, posterior margin angularly produced; merus broadening distally, with both margins slightly stepped at spine bases, anterior margin spined at 0.16 (1+1), 0.28 (2), 0.49 (3), 0.75 (3), and 0.95 (3), posterior margin spined at 0.16, 0.26, 0.46, and 0.70, posterodistal angle with 1+1 spines; carpus margins subparallel, anterior margin scalloped, spined at 0.11 (2), 0.30 (3), 0.62 (3), and 0.92 (3), posterior margin straight, with small spines at 0.27 and 0.73; propod narrowing slightly distally, both margins stepped, anterior margin spined at 0.19 (2), 0.33 (2), 0.49 (2), 0.67 (1), and 0.89 (2), posterior margin spined at 0.24 (3), 0.39 (3), 0.55 (3), 0.75 (3), and 0.93 (2), posterodistal angle with 3 spines. Penal organs subsquare, do not abut in midline.

Epimeral plates: First: triangular, posterior margin with small emargination distally, 2 minute spines proximally. Second: subsquare but with anterodistal angle rounded, posterior margin similarly emarginated, with 3 minute spines. Third: squarer than others, smaller than second, posterior margin with a more pronounced emargination or notch distally, 6 or 7 minute spines posteriorly.

Pleopod 1: biramous, but comparatively short, fine and delicate, peduncle tapering distally, with 1 coupling spine, margins otherwise naked, rami of about equal length, segmentation not obvious, setae sparse. Pleopod 2: reduced to a vestigial cylindrical stump bearing a single spine. Pleopod 3: even more reduced than second, a short triangular vestigial stump.

Uropod 1: comparatively short and dumpy, peduncle with 2 rows of spines dorsally, no inter-ramal spur present, rami equal in length, outer naked, inner weakly spined with 4 spines dorsally. Uropod 2: peduncle with a distinctive spine group dorsodistally, both rami short, spined. Uropod 3: uniramous, peduncle with 1 spine dorsally. Telson: bilobed but not very cleft, with 3 marginal spines on each lobe.

Female: as for male except where specified:

Length 11.1 mm, width 1.65 mm, depth 2.00 mm. Antenna 1: length 1.30. Antenna 2: length 3.87 mm, peduncle segment 3 with a spine at superodistal angle, inferodistal angle with 3 spines; segment 4 superior margin spined at 0.5, superodistal angle with 2-3 spines, inferior margin spined at 0.30 (1) and 0.60 (2), inferodistal angle with 1 small spine; segment 5 superior margin spined at 0.27 (1), 0.44 (1), 0.64 (2), and 0.84 (2), superodistal angle with 2 spines, inferior margin spined at 0.18 (2), 0.35 (2), 0.56 (2) and 0.74 (2), inferodistal angle with 1 spine; flagellum of 17 podomere segments.

Mouthparts: Mandible: incisor 7-cuspate, lacinia mobilis 5-cuspate, 3 pairs of interdentate pilose setae. Upper lip: like male in being less densely setose than usual.

Gnathopod 1: basos broader proximally, spines on anterior margin become larger distally; merus posterior margin not produced; propod narrower; dactyl extends beyond propod margin.

Gnathopod 2: broodplate narrowing distally, with a rounded distal end, 8 spines distally, not curl-tipped; basos anterior margin slightly sinuous, spined at 0.12, 0.23, 0.33, 0.55 and 0.94, posterior margin straight, posterodistal angle with 1 spine; ischium long, curved anteriorly, posterodistal angle with 2 spines; merus posterior margin produced into a pellucid lobe with 4 large spines around its base; carpus posterior margin produced to a pellucid lobe, anterodistal angle with 2 spines; propod long, narrow and mitten-shaped, anterior margin sinuous and naked, posterior margin produced to a pellucid lobe (folded back in slide), lateral face has about 12 large spines in a longitudinal row on the outer face, and 2 longitudinal rows of about 10 spines each on the inner face, palm short, flanked by a group of spines, dactyl short, occludes into a propod pellucid lobe which extends beyond it distally.

Peraeopod 1: broodplate rounded distally, with 9 setae; basos broader distally, anterior margin rounded, naked; propod anterior margin spined at 0.13 (1), 0.32 (2), 0.61 (2), and 0.88 (2), posterior margin spined at 0.16 (1), 0.24 (3), 0.47 (3), 0.64 (3), 0.72 (3), 0.84 (3), and 0.91 (1). Peraeopod 2: broodplate with 8 setae distally; propod anterior margin produced distally into a slight pellucid lobe; dactyl emargination of inner surface as marked. Peraeopod 3: broodplate with 5 setae, rolled margin extends only about 0.33 along length. Peraeopod 3: broodplate with 5 setae, rolled margin extends only about 0.33 along length; basos longer and broader than in male. Peraeopod 4: basos long and ovate, posterior margin smoothly convex. Peraeopod 5: basos posterior margin has larger spines.

Remarks

Waematau unuwhao is very rare. In spite of extensive searching through all the very extensive collections held by museums and government departments I have only encountered 5 specimens in the one collection made by Mr K.A.J.Wise in 1967. In view of the extensive land modification which has taken place in the past, and which is still taking place today, in the general vicinity of where it lives, or lived, I would not be at all surprised if this species is now extinct. I was unable to find it when I collected in the area in 1972.

It is easily recognised by the short antennae 2, the massive and distinctive male second gnathopod, the vestigial nature of pleopods 2 and 3, the naked outer ramus of uropod 1 and the sparse spination on the inner ramus, the spination on both rami of uropod 2, and the marginal, not coronal, spines on the telson.

As in many species, the mature female in this species has broader basos segments on the gnathopods and anterior peraeopods than has the male. Possibly this allows the eggs in the brood to be manipulated and held during brooding. The egg size and average brood size are unknown but the brood probably consists of a few, large eggs, since species in which the broodplates (oostegites) are as reduced as they are in this species have broods of this kind. Possibly, larger eggs are not held as well by oostegites as are small eggs, and so additional mechanisms for holding them are required, thus the development of these broad basos segments in the gnathopods and anterior peraeopods.

Waematau espiratus new species

Figures 301 to 321

Types: The holotype male and allotype female were collected from a forest remnant 5 km south-east of Unuwhao, North Cape area, at 183 m, 24/XI/1967, by K.A.J.Wise, and have been deposited in the Canterbury Museum. (Author's catalogue no. KD 904).

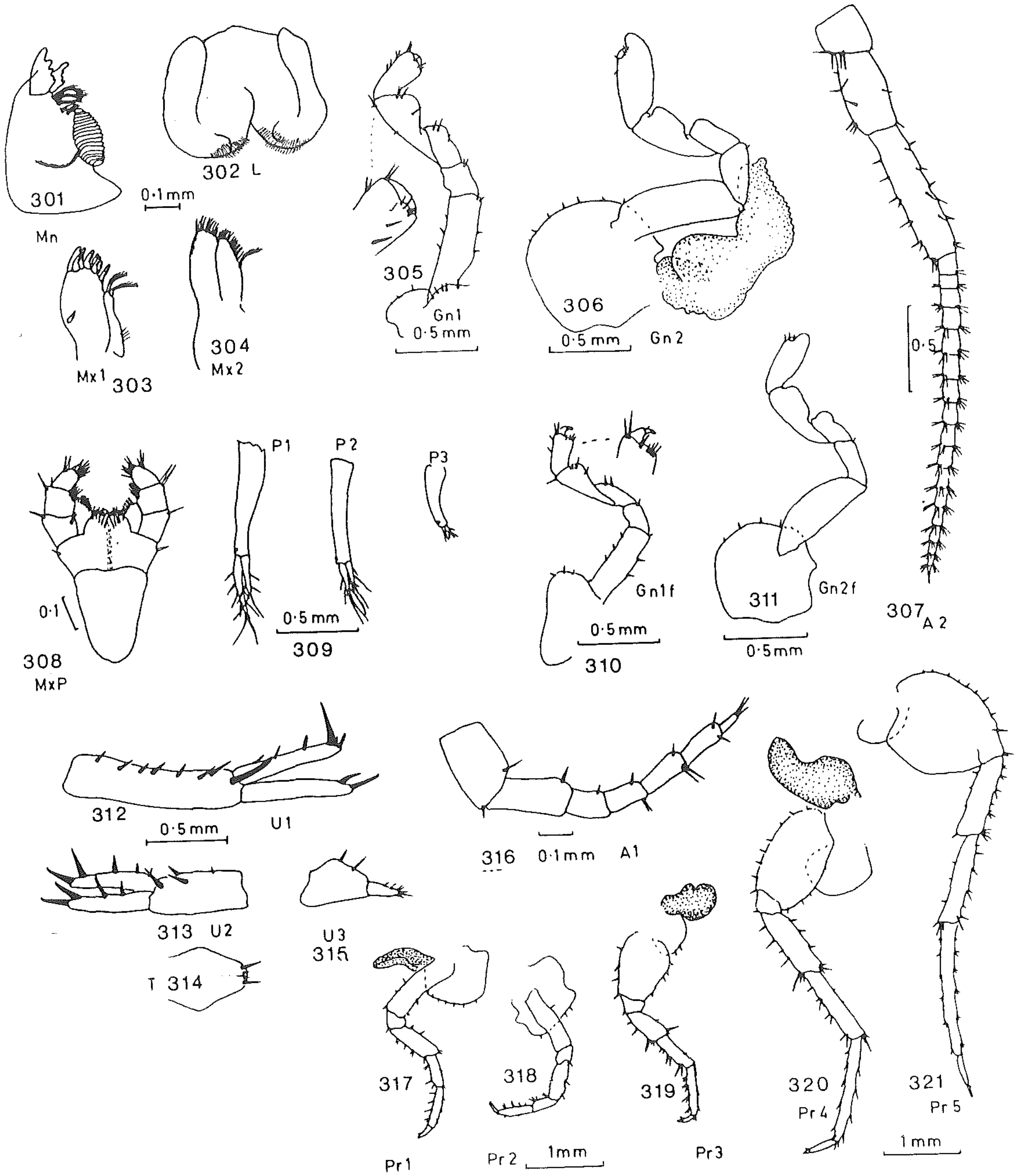
Localities:

East Spirits Bay, Unuwhao, Northland, B.A.Holloway, 29/XI/1960, ovigerous female and 1 male, taken with 2 small *Talitroides topitotum*. Forest remnant, 5 km south-east of Unuwhao, North Cape area, Northland, 183m, 24/XI/1967, K.A.J.Wise. (Type locality).

Etymology. The specific epithet is derived from the type locality.

Diagnosis:

A small to moderate-sized landhopper of the genus *Waematau* with a moderately long, comparatively slender antenna 2; eyes round; gnathopod 1 chelate in both sexes; gnathopod 2 mitten-shaped in both sexes; peraeopods comparatively short; gills large with the last pair each having a long finger-like pendulous lobe; pleopods reduced, the first and second biramous, slender, and sparsely setose, pleopod 3 vestigial in that it is reduced to a cylindrical stump; uropod 1 has a large inter-ramal spur which extends 0.5 length of the rami, outer ramus naked, inner ramus feebly spined dorsally, both rami with very long terminal spines; uropod 2 rami



FIGURES 301-321. Waematau espiratus. 301, mandible. 302, lower lip. 303, maxilla 1. 304, maxilla 2. 305, male gnathopod 1 and gnathopod 1 propod. 306, gnathopod 2 male. 307, antenna 2. 308, maxilliped. 309, pleopods 1,2 & 3. 310, female gnathopd 1 and gnathopod 1 propod. 311, gnathopod 2 female. 312, uropod 1. 313, uropod 2. 314, uropod 3. 315, telson. 316, antenna 1. 317, peraeopod 1. 318, peraeopod 2. 319, peraeopod 3. 320, peraeopod 4. 321, peraeopod 5.

both strongly spined dorsally and terminally.

Description:

Male:

Pigmentation unknown. Length 11.0 mm, width 1.66 mm, depth 1.54 mm. Antenna 1: peduncle segment 1 broadening distally, spined at supero- and inferodistal angle; segment 2 length equals segment 1, broadening distally, superodistal angle with 1 minute spine, inferodistal angle with 1 spine; segment 3 short, curved inferiorly, superodistal angle with 1 minute spine, inferodistal angle with 1 spine; flagellum of 5 podomere segments, podomere segments 1, 2 and 3 each have 3 spines superodistally, and 1-2 spines inferodistally; penultimate segment spines obscure last segment. Antenna 2: peduncle segment 3 short, superior margin convex, with 1 minute spine at superodistal angle, inferodistal angle with a patch of 5 spines; segment 4 broadening distally, longer than segment 3, superior margin spined at 0.41 (1) and 0.81 (3), inferodistal angle with 1 spine; segment 5 long, broadening distally, superior margin scalloped, spined at 0.12 (1), 0.29 (1), 0.45 (2), 0.65 (3), 0.75 (3), and 0.93 (1), superodistal angle with 2 spines, inferior margin spined at 0.18 (2), 0.35 (2), 0.49 (2), 0.58 (2), 0.74 (2), and 0.86 (2), inferodistal angle with 2 spines; flagellum of 17 podomere segments, not very tapering, each podomere segment except the last has 3 spines at each of the 4 distal angles, terminal tuft on last segment short and sparse.

Mouthparts: Upper lip: ventral margin circular, pilose. Mandible: incisor a linear, saw shape, 5-toothed, lacinia mobilis

4-toothed, 4 interdentate pilose setae, setal tuft present, molar 19-striate, molar medial seta present, pilose but shorter than usual. Lower lip: has normal scroll shape but setae limited to a region of the distal inner margin. Maxilla 1: inner plate narrow, tapering distally, terminates in 2 long pilose setae; outer plate broader, margins subparallel, curved inwards distally, terminates with a row of 8 spine teeth bearing 2, 2, 4, 4, 4, 4, 4, 4 lateral teeth (from outer to inner); a small palp is present towards outer margin. Maxilla 2 inner plate distal margin acutely angled so that plate is almost triangular, distal margin has a row of setae terminating proximally with a long pilose seta; outer plate curved somewhat inwardly, distal margin convex, with a row of setae. Maxilliped: lost.

Gnathopod 1: coxal plate ventral margin rounded, with 5 spines; plinthic ridge present with 5 large spines; basos broadening distally, anterior margin straight, spined at 0.48, 0.65, and 0.76, posterior margin convex, slightly scalloped between first and second spine groups, spined at 0.43, and 0.63, posterodistal angle with 2 spines; basos subsquare, anterior margin scarcely produced, posterior margin slightly convex, posterodistal angle with 2 spines; merus posterior margin produced mesodistally into a discrete, rounded pellucid lobe guarded at its base by 3 large spines; carpus anterior margin long, spined at 0.51, anterodistal angle with 5 long spines, posterior margin is produced to a large pellucid lobe, guarded proximally by 1 spine on one face and 2 on the other, and distally by 3 large spines at the posterodistal angle; propod broadening distally, anterior margin stepped slightly spined at 0.60 (3), and 0.86 (3), anterodistal angle with 5 long spines, posterior margin produced into a pellucid lobe guarded at its base by a row of 7 spines on each face, the pellucid lobe is produced a little beyond palmar area posteriorly, palm transverse, ends short of propod posterior margin, flanked on each side by a row of spines which are biggest at the beginning and at the end of the palm; finger short, less than propod width, tip appears to occlude a short extension of the propod pellucid lobe.

Gnathopod 2: coxal plate ventral margin rounded with about 6 strong spines; gill comparatively large, trilobed, anterior lobe hooked, anterior margin crenulate; basos broad, anterior margin convex, naked, posterior margin posterior margin slightly sinuous, posterodistal angle with 1 small spine; ischium comparatively long, broadening slightly distally, posterodistal angle with 2 small spines; merus posterior margin produced into a pellucid lobe guarded by a few small spines at its base; carpus anterior margin long, naked, posterior margin produced into a pellucid lobe, posterodistal angle with 1 small spine; propod mitten-shaped, margins subparallel, straight and naked, palm short, flanked by a row of spines, palmar angle 43^{o}, anterodistal angle with 2 spines, a longitudinal row of about 8 spines runs along the propod face, posterior produced distally into a lobe which extends well beyond palmar area; dactyl short, appears to occlude pellucid lobe of propod.

Peraeopod 1: coxal plate ventral margin convex, with 7 spines; gill discoidal; basos curved anteriorly, anterior margin concave, spined at 0.58, 0.70, 0.77, and 0.90 (2), posterior margin convex, slightly scalloped, with larger spines at 0.29, 0.53, and 0.71, posterodistal angle with 1 larger spine; ischium anterior margin produced slightly, posterior margin nearly straight, posterodistal angle with 1 spine; merus broadening distally, anterior margin spined at 0.13, and 0.39, anterodistal angle with 2 large spines, posterior margin spined at 0.32 (2), 0.52 (2), and 0.79 (2), posterodistal angle with 2 spines; carpus curved slightly posteriorly, anterior margin spined at 0.29 (1), and 0.47 (2), anterodistal angle with 1 spine, posterior margin scalloped, with larger spines in 0.11, 0.31, 0.57, and 0.80, posterodistal angle with 2 large spines; propod curved posteriorly, both margins stepped, anterior margin spined at 0.21, 0.51, and 0.77, anterodistal angle with 2 spines, posterior margin with larger spines at 0.23 (3), 0.38 (3), 0.57 (3) and 0.85 (3), posterodistal angle with 1 small spine; dactyl comparatively long, inner margin slightly emarginate.

Peraeopod 2: coxal plate ventral margin nearly straight, with about 6 spines, anterodistal angle rounded; basos margins subparallel, curved a little anteriorly, anterior margin naked, posterior margin with 2 large spines at 0.22 and 0.37; ischium anterior margin slightly produced, posterior margin straight, with 1 spine at posterodistal angle; anterior margin spined at 0.50, anterodistal angle with 1 spine, posterior margin spined at 0.24, 0.45 and 0.90 (2), distal margin flanked by 3 large spines; carpus anterior margin naked, anterodistal angle with 1 small spine, posterior margin scalloped, with large spines at 0.38 (2), posterodistal angle with 3 large spines; propod with both margins stepped, anterior spined at 0.37 (2) and 0.75 (2), anterodistal angle with 4 large spines, posterior margin scalloped, spined at 0.21 (1), 0.34 (2), 0.55 (3), and 0.81 (3), posterodistal angle with 1 spine; dactyl inner margin slightly emarginate.

Peraeopod 3: coxal plate: and with both lobes rounded, with 3 spines each; gill discoidal; basos an inverted pyriform-shape, anterior margin with large spines at 0.40 (1), 0.51 (1), 0.63 (2), 0.82 (2), anterodistal angle with 2 spines, posterior margin with small spines at 0.19, 0.37, 0.49, 0.60, and 0.84, posterodistal angle with 1 spine; ischium anterodistal angle with 1 spine, posterior margin slightly produced; merus anterior margin scalloped, spined at 0.26 (2), 0.49 (3), and 0.79 (3), posterior margin spined at 0.60, posterodistal angle with 1 large spine; propod with both margins stepped but particularly the anterior which is spined at 0.16 (2), 0.36 (2), 0.59 (2), and 0.84 (4), posterior margin spined at 0.50 and 0.81, posterodistal angle with 1 spine; dactyl inner margin slightly emarginate. Peraeopod 4 coxal plate ventral margin rounded, naked; gill comparatively small, pendulous lobe short and blunt; basos ovoid; ischium anterodistal angle with 2 spines, posterior margin short; merus broadening distally, anterior margin stepped, spined at 0.23 (2), 0.43 (2), 0.57 (1), and 0.71 (2), anterodistal angle with 4 spines, posterior margin stepped, spined at 0.18, 0.35, and 0.69, posterodistal angle with 3 spines; carpus broadening distally, anterior margin stepped, spined at 0.22 (2), 0.40 (3), and 0.63 (3), anterodistal angle with 3 spines, posterior margin slightly scalloped, spined at 0.28 (2), 0.48 (1), and 0.73 (1), posterodistal angle with 4 spines; propod long, not tapering, both margins stepped, anterior margin spined at 0.15 (1), 0.25 (2), 0.42 (3), 0.64 (2), and 0.91 (3), posterior margin spined at 0.18 (1), 0.28 (3), 0.49 (2), 0.72 (1), and 0.91 (19, dactyl long, conical. Peraeopod 5: coxal plate anterodistal angle very rounded, margins naked; basos broader than long; ischium anterodistal angle with 2 spines; merus broadening slightly distally, both margins stepped, anterior margin spined at 0.13 (1), 0.21 (2), 0.43 (3), 0.59 (1), and 0.70 (3), anterodistal angle with 4 spines, posterior margin spined at 0.14, 0.32, and 0.58, posterodistal angle with 3 spines; carpus anterior margin stepped, spined at 0.12 (1), 0.21 (2), 0.38 (3), 0.59 (3), and 0.78 (1), anterodistal angle with 3 spines, posterior margin nearly straight, spined at 0.31, 0.49, and 0.73, posterodistal angle with 3 spines; propod long, curved slightly anteriorly, tapering slightly, both margins stepped, anterior margin spined at 0.07 (1), 0.21 (2), 0.35 (3), 0.51 (3), 0.70 (3), and 0.90 (3), posterior margin spined at 0.07 (2), 0.23 (3), 0.38 (3), 0.56 (3), 0.75 (3), and 0.94 (1); dactyl long, narrow, and conical.

Pleopod 1: length (excluding terminal spines) 1.13 mm, peduncle margins naked, 1 coupling spine on inner margin; rami reduced to few (5) segments although segmentation is difficult to determine, inner ramus longer than outer. Pleopod 2: length 0.86 mm, peduncle margins naked with 2 coupling spines, rami reduced to short stumps of about 3 segments, inner ramus is slightly larger. Pleopod 3: very reduced, length 0.41 mm, peduncle narrowing distally, with 2 small coupling spines, both rami reduced to 1-segmented triangles, sparsely setose.

Uropod 1: peduncle with 7 large spines in 1 row dorsally, large inter-ramal spur present; outer ramus naked, terminating with 1 very large scionate and 1 small spine; inner ramus weakly spined with 3 dorsal spines, terminating in 1 very long, scionate spine and 2 smaller spines. Uropod 2: peduncle with 3 spines dorsally, inter-ramal spur present; each ramus spined dorsally, and terminating with 2 longer and 1 shorter spine. Uropod 3: forms faecal guide, uniramous, peduncle with 2 marginal spines, ramus has very characteristic spination with 2 dorsal, 3 terminal spines which are directed upwards and 3 longer spines directed backwards. Telson: only slightly cleft, with 1 large and 1 small spine on each lobe.

Female:

Non-ovigerous and possibly immature. As for male except where noted

Length 9.41 mm, width 1.24 mm, depth 1.53 mm. Antenna 1: extends to 1/4 along antenna 2 peduncle segment 5, flagellum of 5 podomere segments of which the first is slightly curved superiorly and the third is longest. Antenna 2: flagellum of 14 podomere segments. Mouthparts: Maxilliped: not very broad, palps comparatively narrow, palp segment 4 present, partly obscured by segment 3.

Gnathopod 1: propod narrower and palm shorter than in male. Gnathopod 2: propodal distal lobe not as produced as in male, palmar angle slightly more obtuse.

Remarks

I designate the female specimen as an allotype with reluctance since it is non-breeding and rather small. Such specimens do not show the breeding oostegites which are important characters. Nor do they show the full development of the sexually dimorphic characters. The small size of the females probably explains the marked similarity between the sexes with the only reliable sexual character being the presence or absence of penal plates. However, because no larger or better specimens are present in the collections available and because the species may well now be extinct, I feel justified in nominating both a holotype and an allotype even though the two are very similar and small.

Genus *Parorchestia* Stebbing, 1899: 402.

Parorchestia Stebbing, 1906:557; Shoemaker, 1942:17; Bousfield, 1964:50.

Orchestia Hurley, 1957:149.

Like *Waematau* with naked peduncle outer margins on pleopods, body fine, antenna 2 delicately spined and tapering, and uropod 1 outer ramus naked, but with uropod 2 outer ramus also naked. Truly inland species found far from the shore with some species feminized and some with reduced pleopods.

Type species: *Orchestia tenuis* Dana, 1852.

Other species: *P.lesliensis* (Hurley, 1957); *P.ihurawao*, new species; *P.longicornis* new species erected from a form of *P.stewarti* Stephensen, 1938.

Remarks

Stebbing erected this genus to receive *tenuis*, *hawaiensis*, and *sylvicola*. Both *sylvicola* and *hawaiensis* are excluded by the definition above. They are more primitive species which are best placed in other genera (*Tara* for *sylvicola*, while *hawaiensis* must remain in *Orchestia* until the next reviewer places them in a more natural genus). Stephensen (1935) included a number of species of *Parorchestia* which are excluded by this definition. The New Zealand species in his grouping have been dealt with earlier in this work, but those beyond New Zealand need formal regrouping. Certainly, *Parorchestia* should be regarded as a genus endemic to New Zealand.

Parorchestia tenuis (Dana, 1852)

Figure 322

Parorchestia tenuis Stebbing, 1899:402; Stebbing, 1906:557-558; Chilton, 1909:642; Chilton, 1911:565; Stephensen, 1935:14; Shoemaker, 1935:6; Bousfield, 1964:45.

Orchestia tenuis Dana, 1852:202; Dana, 1853, 1855:872; Spencer Bate, 1862:29; Stebbing, 1899:402; Hurley, 1957:166-172.

Distribution:

Throughout New Zealand (North, South and Stewart Islands) with the exception of the east coast of the South Island north of Dunedin and south of Seddon. There is a dubious record given by Chilton (1909) from the mouth of a fresh water stream on Campbell Island. *P.tenuis* is not usually coastal and is not found in freshwater, and since Chilton's specimens were small and therefore difficult to identify, the record from the subantarctic islands is suspect.

The material examined includes 1820 tubes held in the collections of the Otago, Canterbury, Auckland and National Museums, the British Museum of (Natural History), and the B.P.Bishop Museum, Honolulu, Hawaii. Collectors include: R.R.Forster, S.Duncan, C.L.Wilton, B.Sutherland, P.M.Johns, D.A.McHugh, F.M.Climo, R.S.Bigelow, D.Tattle, C.J.Burrows, J.Sutherland, J.T.Salmon, P.C.Bull, J.Sorenson, C.Lindsay, R.G.Ordish, P.D.Gear, B.A.Holloway, R.K.Dell, G.Weston, J.Barnett, J.Ramsay, A.J.Healy, A.C.O'Connor,

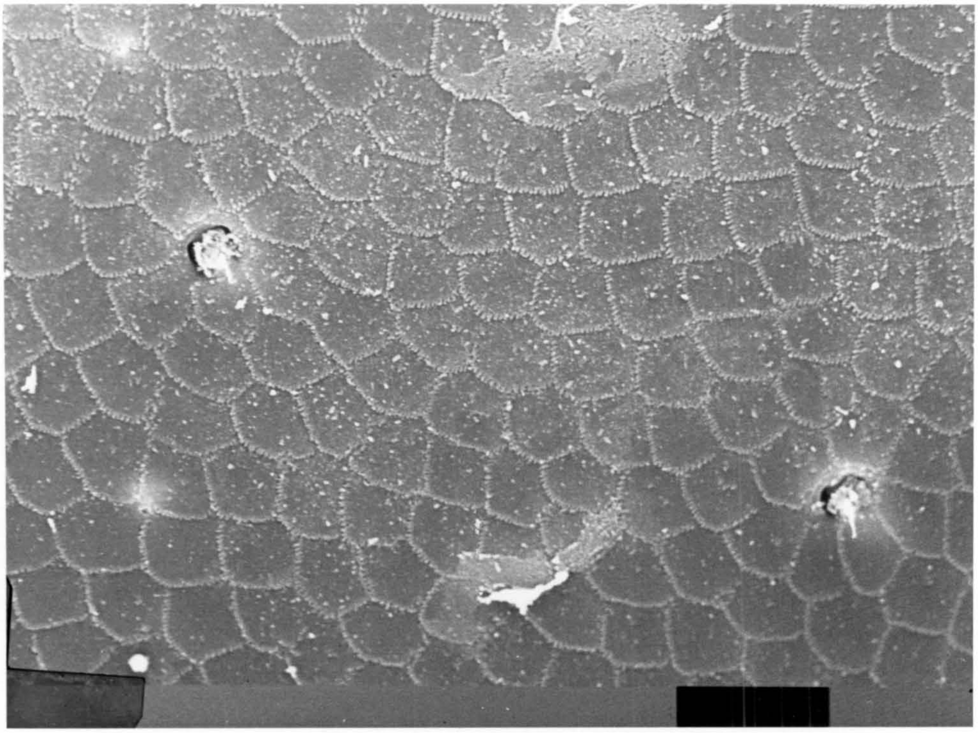


FIGURE 322. Cuticular structures of <u>Parorchestia</u> <u>tenuis</u>. The micrograph is of the midlateral surface of thoracic segment 2. Macropores open in dermal gland polygons and show mucoid remains in their ducts. Cuticular polygons are well defined and mesopores are arranged in a single row or arc at the posterior margins of the polygons. These mesopores are overhung by 'verandas'. The scale bar indicates 20 micrometres.

D.Hurley, J.H.McMillan, J.M.Moreland, G.Caughley, Vernon Stout, M.M.Davidson, K.A.Wodzicki, L.C.Hudson, B.E.Sutherland, B.Beatson, J.Kikkawa, A.Chapman, E.G.Turbott, R.Rowe, P.R.Kettle, Moyra Seden, F.C.Kinskey, R.A.Falla, J.A.Bartle, L.C.Cadenhead, N.A.Deans, C.L.McLay, E.E.Calver, K.A.J.Wise, K.Fox, A.K.Walker, J.S.Dugdale, J.C.Watt, W.Kuschel, T.K.Crosby, C.Mitchell, and myself.

Remarks

Parorchestia tenuis is one of the most common New Zealand landhoppers. It is generally found away from the coast in more inland areas where it ranges in altitude from near sea-level to well above bush-line. It occupies northern kauri-hardwood- softwood communities, kanuka-manuka catastrophe communities, beech forests and alpine grasslands. It appears to be an aggressive coloniser, rapidly recolonising areas after catastrophes. Thus it is found throughout the area devastated by volcanic ash showers and lava flows in North Island. However, it does not occupy the drier regions that *M.hurleyi* and *Talorchestia aotearoa* do. It is really abundant only in areas of regular, plentiful rainfall such as occur throughout most of North Island and the west coast of South Island.

P.tenuis is an easily identified, brightly red coloured, reticulated species. It lives in a variety of situations including under stones on river banks, a habit that may explain why Chilton recorded it as a fresh water species. When *P.tenuis* is disturbed in such riparian situations it sometimes hops into the water where its frantic efforts to get out attract attention and make it easy to collect. However, it is not a fresh water animal even though it lives in low conductivity soils in environments which can be very damp. In fact, like all true landhoppers, if it is held under water it drowns. The North Island, Nelson, West Coast and Catlins specimens seem to differ slightly in details of spination from the Fiordland and Stewart Island specimens. As yet, these details are not sufficient to warrant separation at the species level. It may be that future collections and study will reveal that P.tenuis is a species complex rather than a simple taxon.

Parorchestia lesliensis (Hurley, 1957)

Figure 323

Orchestia lesliensis Hurley, 1957:172-174.

Localities and collectors:

Leslie Valley Track, Nelson, R.R.Forster, 23/I/1948, in beech forest. Blue Mountains, Silverstream, Wellington, J.T.Salmon, 18/VIII/1948, West Longwood Range, Southland, G.C.Watson, 13/III/1948. Alford Forest Scenic Reserve, Staveley, Canterbury, 43°37'S 171°30'E, P.M.Johns, 26/III/1968, ex Nothofagus litter. Kaituna Valley, Banks Peninsula, MC.,N.Z., P.M.Johns, 16/IV/1977, in Fuchsia-ngaio litter, taken with Makawe hurleyi. Mt Fitzgerald Scenic Reserve, MC.,N.Z., M.C.Crawley, 1/IX/1977, litter in relict totara forest, taken with M.hurleyi. Coopers Knob, Banks Peninsula, MC.,N.Z., P.M.Johns, 7/III/1977, in Fuschia litter. Hump Ridge, Southland, 2743-3200 m, P.M.Johns, 19/X/1969, under stones. Ahuriri Scenic Reserve, Coopers Knob, Banks Peninsula, R.S.& N.S.Bigelow, 26/XI/1976. Peel Forest, R.Forster, 10/II/1946, leafmould.

Remarks

This upland species occurs discontinuously on hills and mountains throughout the east coast of the South Island and, apparently, the south of the North Island. I have not been able to confirm its occurrence in the North Island in spite of extensive searching. It probably once had a continuous distribution and has been restricted to relict patches by climate changes - if it is a cool climate species - or by competition from other species.

It is easily identified by its reticulated body pattern, the vestigial third pleopod, and the characteristic gnathopods.

I have not been able to inspect the types as they have not been lodged in the National Museum and cannot now be located.

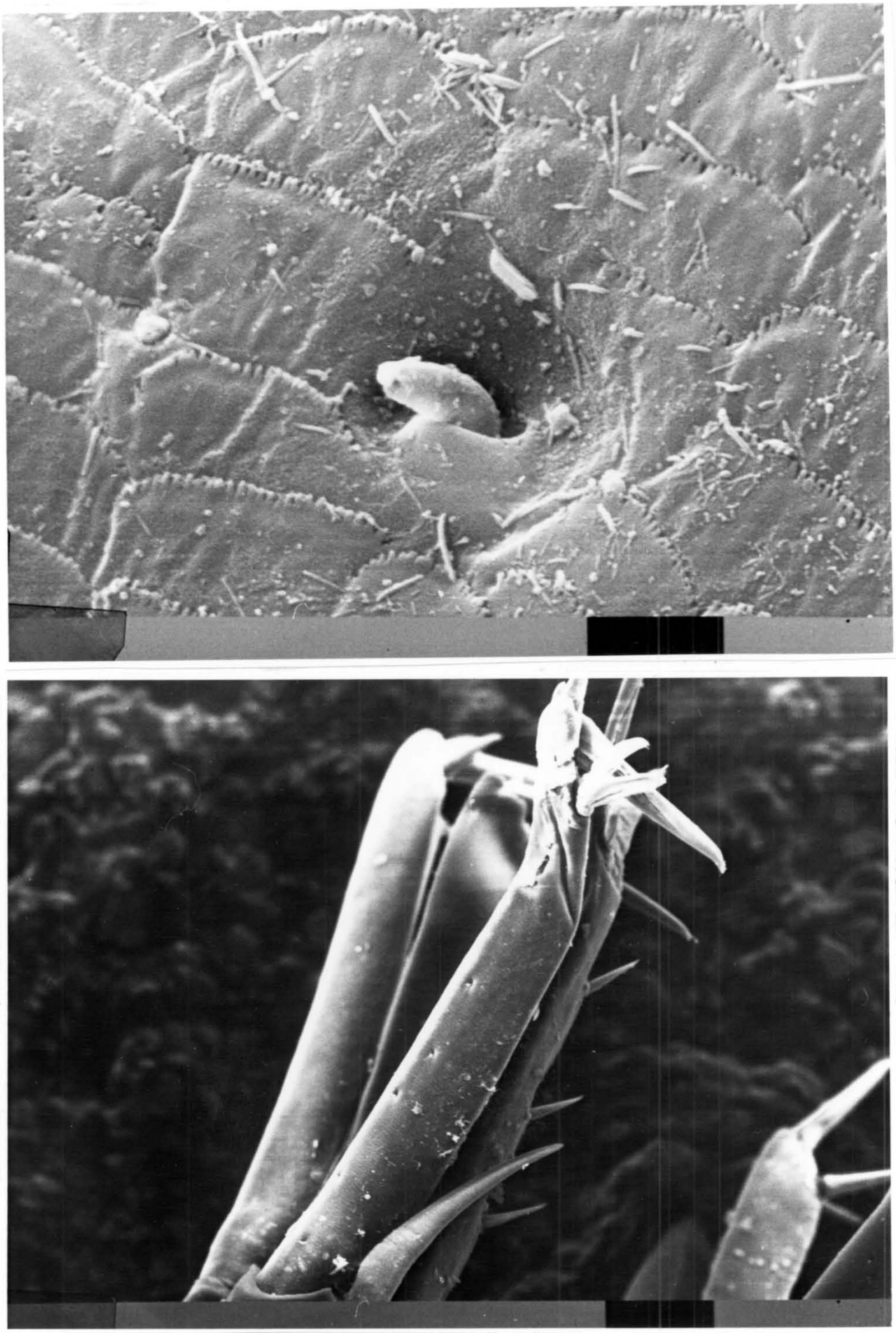
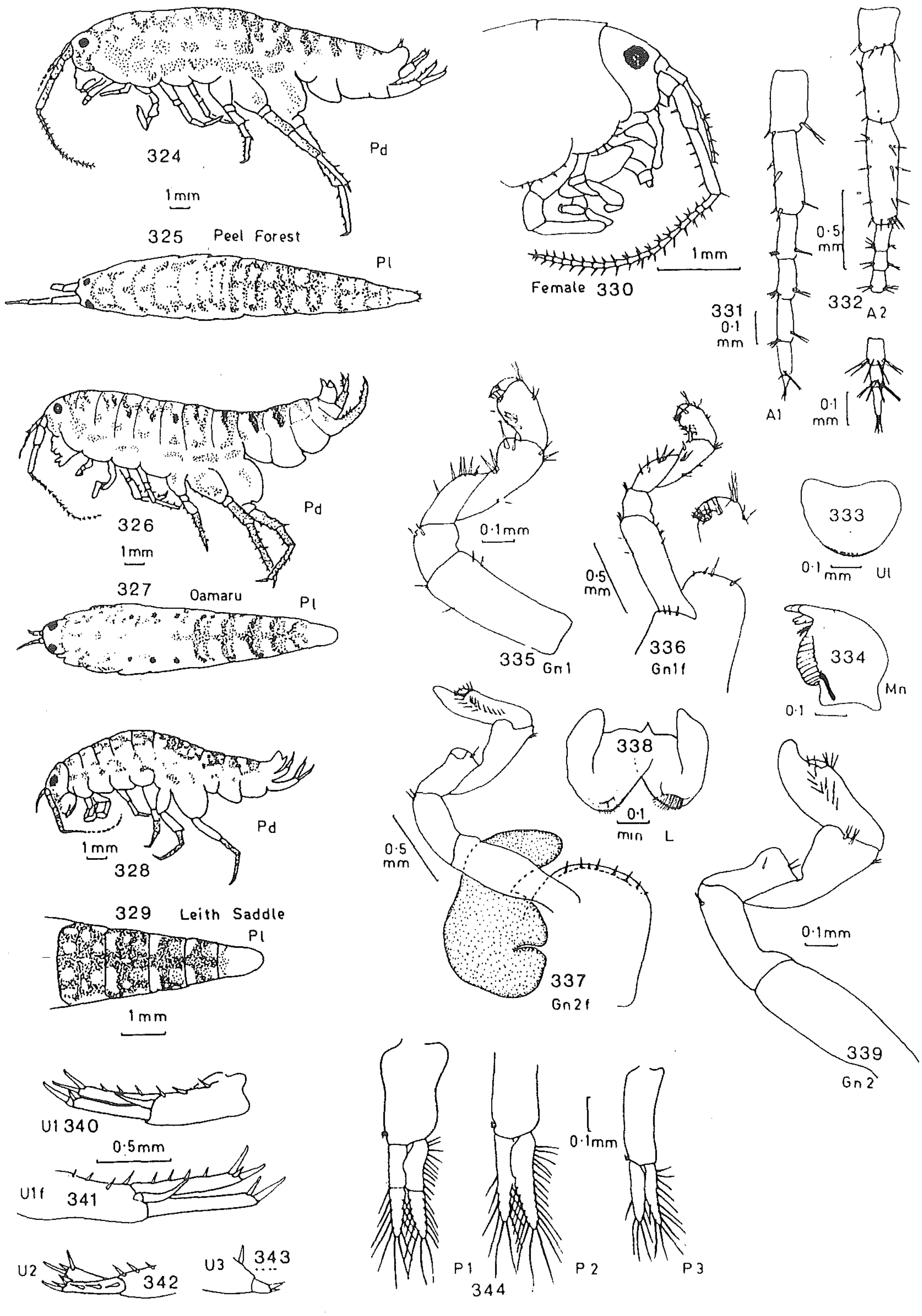


FIGURE 323. Cuticular structure of Parorchestia lesliensis. The upper micrograph is of the midlateral surface of thoracic segment 2. It shows a large macropore opening into a dermal gland cell cuticular polygon with a mass of mucoid material in the duct. The cuticular polygons of the epidermal cells are well defined but are more rectangular than polygonal. In particular, the mesopore arcs are nearly straight on most of the cells. The mesopores are overahung by 'verandas'. The scale bar indicates 3.5 micrometres.

The lower micrograph shows the uropods on the same specimen. Note the large macropores. The scale bar indicates 70 micrometres.



FIGURES 324-344. Parorchestia ihurawao.
324, lateral aspect of specimen from Peel Forest. 325, dorsal aspect, Peel Forest specimen. 326, dorsal aspect of specimen from Oamaru. 327, lateral aspect, Oamaru specimen. 328, lateral aspect of specimen from Leith Saddle. 329, dorsal aspect, Leith Saddle specimen. 330, cephalon. 331, antenna 1. 332, antenna 2. 333, upper lip. 334, mandible. 335, gnathopod 1 male. 336, gnathopod 1 female. 337, gnathopod 2 female. 338, lower lip. 339, gnathopod 2 male. 340, uropod 1 male. 341, uropod 1 female. 342, uropod 2 male. 343, uropod 3 male. 344, pleopods 1,2 & 3.

Parorchestia ihurawao new species

Figures 324 to 344

Types:

The holotype male and allotype female were collected from Peel Forest, South Canterbury, South Island, New Zealand, 43°54'S, 171°15'E, and have been deposited in the Canterbury Museum.

Etymology: the specific epithet means "from 'peel' or 'uncover' forest" in Maori.

Diagnosis:

A weakly sexually dimorphic land hopper of the genus *Parorchestia*, with a semi-reticulated body pattern in alcohol which defines prominent yellow superolateral dots; eyes large, black; antenna 1 extends to between 0.33 and 0.5 along antenna 2 peduncle segment 5; antenna 2 short, not very tapering, delicately spined; gnathopod 1 chelate in both sexes; gnathopod 2 mitten-shaped in both sexes; peraeopods comparatively short and stout; pleopods all present, biramous, broad, margins pilose or setose, with 2 coupling spines present; uropod 1 outer ramus naked, with a long inter-ramal spur reaching 0.5 along rami; uropod 2 outer ramus naked.

Localities and collectors:

Woodhall Gardens, Dunedin, S.Duncan, 21/VIII/1977, 4M, 4F, taken with *Makawe hurleyi*. Whare Flat, Dunedin district, C.L.W.(Wilton?), 4/I/1966, ex nigger head, taken with *M.hurleyi*. Wainakarua Reserve, North Otago, S43 3439, K.W.D., 27/VIII/1977, 2F taken with M.hurleyi. Leith Valley, Dunedin, S.Duncan, 21/VIII/1977, in leaf litter, 1F taken with a number of M.hurleyi. Goodwood Scenic Reserve, North Otago, K.W.D., 27/VIII/1977, 1F taken in cattle-damaged bush with many M.hurleyi. Leith Valley, Dunedin, K.W.D., 21/VIII/1977, leaf litter, 10F, 1M, 6 M.hurleyi. Kelseys Bush, South Canterbury, S44 5314, K.W.D., 27/VIII/1977, in Fuchsia litter. Glentaki, N.Bank of Waitaki R., S.Duncan, 20/VIII/1977, in grass litter, 3 small individuals taken with M.hurleyi. Silver Peaks, 15 km N of Dunedin, D.A.McHugh, 30/IX/1967, 1F, 1 imm. Upper Gardens, Opoho, Dunedin, K.W.D., 6/IX. in kanuka (Leptospermum ericoides) litter. Hapuku Scenic Reserve, 42°20'S 173°44'E, Kaikoura District, K.W.D., 3/IX/1977, males smaller but as numerous as females. Kowhai Bush Reserve, Kaikoura district, K.W.D., 2/IX/1977, in grass litter at bush edge, none found in bush. Peel Forest, bush margin, K.W.D., 25/V/1969,. The Cabstand, Akaroa, Banks Peninsula, P.M.Johns, 1/X/1974, in Nothofagus litter. Okaratahi Bridge, N of Conway, C.L.W., 22/IX/1967, 3F. Station 1, Dunback-Macraes Road, SW3 1931, C.L.Wilton, 24.IX.1967, 5F, 2M. Deep Dell, S43 0332, C.L.Wilton, 4/XI/1967, 12F, 9M. Opoho Bush, Dunedin, C.L.W., 10/XII/1970, many F, 1M, taken with many M.hurleyi and 2 T.patersoni. Bracken slope above river, Wainakarua, N Otago, B.Beatson, 24/IV/1971, in bracken litter. Near Red Hut, Mt Misery Rd., Wainakarua, N Otago, B.Beatson, 24/IV/1971. Awa-awa-rata Reserve (McLennans Bush), Canterbury, K.W.D., 31/XII/1980, 13 specimens taken in mixed black beech-podocarp-hardwood forest litter. Horse Fall Road, Mt Peel, Canterbury, K.W.D., 2/II/1980, 19

F taken in podocarp-hardwood forest litter. Hapuku Reserve, Kaikoura district, K.W.D., 31/VIII/1981, 7 imm., 8M, 6nbF, 4 bF: brood composition 4e, 3e, 2e, and 3e. Little Akaloa, Banks Peninsula, C.L.McLay, 15/VI/1982, in moss at base of waterfall. Leith Saddle, Dunedin District, K.W.D., 6/V/1983, in regenerating podocarp-hardwood forest. Warren St. Reserve, Oamaru, K.W.D., 6/V/1983, in litter under flax (*Phormium*).

Description:

Male:

Length 6.47 mm, width 1.18 mm, depth 1.50 mm. Pigmentation in alcohol: semireticulated red-brown pattern, with mid-dorsal longitudinal stripe ill-defined on thorax, more definite on abdomen; each segment with two radical hoops merging superolaterally, with a complex series of spots on the thorax midlateral. Colour in vivo: rufous with a glistening, iridescent surface. Eye round, black, nearly 0.5 head capsule length; cheek with 2 prominent spines.

Antenna 1: length 1.27 mm; peduncle segment 2 slightly longer and narrower than segment 1, superodistal angle with 2 small spines, inferodistal angle with 2 large spines; segment 3 with 2 spines on superior margin, superodistal angle with 2 spines, inferodistal angle with 1 large spine; 5 segmented flagellum extends to 0.5 along antenna 2 peduncle segment 5; podomere segments 1 to 4 are all the same length but each is progressively narrower than the preceding one, each has 3 spines superiorly and 3 longer spines inferiorly on distal margins; last segment is short, triangular, with a sparsely setose terminal tuft as long as the segment itself.

Antenna 2: length 3.44 mm; short, not very tapering; peduncle segment 3 distal margin spined laterally and inferiorly; segment 4 superior margin with 2 minute spines, superodistal angle with 1 spine, inferior margin spined at 0.28 and 0.55, inferodistal angle with 1 spine; segment 5, 1.33 times length segment 4, narrowing distally, with 3 groups of spines on superior and inferior margins, distal margin 1 spine superiorly, 2 spines superolaterally, 2 spines inferolaterally, and 1 spine inferiorly; flagellum with 16 podomere segments, each of which except the last has 4 groups of 3-4 fine setae on distal margins; last segment relatively long and conical with a close-bound, sparse terminal tuft.

Mouthparts: Upper lip: distal margin slightly more acutely rounded than usual, finely pilose. Mandible: maxilla 5-toothed, lacinia mobilis 5-toothed, 4 interdentate pilose setae, abmolar setal tuft absent, molar about 13-striate, molar medial seta pilose, about as long as molar width. Lower lip: sparsely pilose distally. Maxilla 1: outer plate with a minute palp, otherwise naked; distal margin with 9 inwardly-curved teeth bearing 0, 1, 1, 3, 3, 3, 3, 3, 3 and 3 lateral teeth (from outer to inner). Maxilla 2: outer plate margins subparallel, outer margin finely pilose, distal margin bearing 15 or so inwardly-curved teeth, inner margin concave distally and pilose; inner plate: more rectangular and less foliaceous than usual with more defined distal margin which bears 18 or so inwardly curved teeth, the spine row terminates at inner margin in a densely pilose long seta, inner margin nearly straight, densely pilose with pilae nearly as long as distal teeth. Maxilliped: lost in type, description based on a male paratype:

inner plate distal margin with 2 large and 1 small spine teeth with pilose setae submarginally and partly down midline; outer plate rounded distally, with a fringing comb of setae set submarginally from inner and distal margins; palp not very broad, segment 4 not obscured by segment 3. Gnathopod 1: basos broadening distally, anterior margin slightly concave, spined at 0.71, 0.82, and 0.89, posterior margin slightly convex, spined at 0.72 and 0.80, posterodistal angle with 2 spines; ischium posterodistal angle with 2 spines; merus posterior margin convex, spined at 0.45, 0.60, 0.79, 0.83, 0.87, and 0.89; carpus broadening distally with the posterior margin produced distally into a pellucid lobe, anterior margin spined at 0.41, anterodistal angle with 4 spines, posteroproximal angle with 2 large spines, poterodistal angle with 2 large spines submarginally; propod broadening distally, anterior margin stepped, spined at 0.73 (2), posterodistal angle with 3 long spines, posterior margin convex but not greatly produced, with 2 longitudinal submarginal rows of 2 and 3 long spines respectively, palm convex, 0.5 propod width, flanked by a row of 5 spines, terminated anteriorly by 2 long spines, palmar angle 92°; dactyl slightly longer than palm, with 2 short spines at base of terminal spine. Gnathopod 2: basos broadest medially; ischium long, posterodistal angle with 1 small spine; merus and carpus both produced posterodistally into pellucid lobes; propod broadest medially, mitten-shaped, anterior margin slightly concave, anterodistal angle with 6 spines, posterior margin convex, produced into a pellucid lobe which projects distally beyond palmar region, palm flanked by about 5 spines, palmar angle 45°; dactyl short.

Peraeopod 1: basos broadening distally, anterior margin spined at 0.67 and 0.90 (2), posterior margin spined at 0.36, 0.49, and 0.79, posterodistal angle with 1 spine; ischium posterodistal angle with 1 spine; merus broadening distally, anterior margin stepped and spined at 0.45, posterior margin nearly straight, spined at 0.24, 0.41, 0.52, 0.69, and 0.90; carpus margins subparallel, anterior margin naked, anterodistal angle with 2 spines, posterior margin scalloped, spined at 0.11, 0.26, 0.36, 0.63, 0.84, and 0.89; propod narrowing distally, anterior margin stepped, spined at 0.42, anterodistal angle with 3 spines, posterior margin scalloped and stepped, spined at 0.26 (1), 0.40 (2), and 0.64 (2).

Peraeopod 2: basos strongly curved anteriorly, anterior margin concave, naked, anterodistal angle with 1 spine, posterior margin convex, spined at 0.48 and 0.71, posterodistal angle with 2 spines; ischium rhomboidal, posterodistal angle with 2 spines; merus broadening distally, anterior margin spined at 0.32, anterodistal angle with 2 spines, posterior margin spined at 0.40, 0.81, and 0.89; carpus anterior margin naked, anterodistal angle with 3 spines, posterior margin scalloped, spined at 0.33 (2), 0.70 (2), and 0.82 (1); propod narrowing distally, anterior margin slightly scalloped, spined at 0.35 (2), and 0.74 (2), anterodistal angle with 4 spines, posterior margin scalloped and stepped, spined at 0.32 (2), 0.49 (2), and 0.74 (2), posterodistal angle with 1 spine.

Peraeopod 3: comparatively short; gill a simple sac; coxal plate lobes spined; basos an inverted pyriform shape, anterior margin spined at 0.22, 0.37, 0.52, and 0.73, anterodistal angle with 2 spines, posterior margin with large spines at 0.51 and 0.79 and small spines at 0.09, 0.22, and 0.44, posterodistal angle with 1 large spine; ischium anterodistal angle with 2 spines, posterior margin slightly produced; merus short, broadening distally, anterior margin spined at 0.40, 0.77, and 0.89, posterior margin spined at 0.35, posterodistal angle with 2 spines; carpus as long as merus, margins subparallel, anterior margin spined at 0.28 (1), 0.47 (2), and 0.79 (3), posterior margin naked, posterodistal angle with 1 large and 2 smaller spines; propod tapering distally, both margins stepped, anterior margin spined at 0.18 (1), 0.32 (2), 0.50 (2), and 0.73 (3), posterior margin spined at 0.47 (2), and 0.75 (2), posterodistal angle with 4 spines.

Peraeopod 4: comparatively short; gill not very large, pendulous lobe short and triangular; coxal plate ventral margin rounded, naked; basos an inverted pyriform shape, anterior margin spined at 0.07, 0.11, 0.23, 0.34, 0.49, 0.64, and 0.82, anterodistal angle with 1 spine, posterior margin spined at 0.56 and 0.82; ischium anterodistal angle with 2 spines; merus broadening slightly distally, both margins stepped, anterior margin spined at 0.27 (2), 0.52 (3), and 0.90 (1), anterodistal angle with 2 spines, posterior margin spined at 0.31 and 0.56, posterodistal angle with 1 long spine; carpus anterior margin scalloped, spined at 0.25 (2), 0.51 (3), 0.79 (1), and 0.87 (3), posterior margin spined at 0.59, posterodistal angle with 3 spines; propod broadest medially, both margins stepped, anterior margin spined at 0.15 (1), 0.30 (3), 0.51 (3), 0.78 (3), and 0.92 (3), anterodistal angle with 1 spine, posterior margin spined at 0.35 (3), 0.58 (3), and 0.87 (3), posterodistal angle with 3 spines.

Peraeopod 5: basos as broad as long, anterior margin spined at 0.23, 0.36, 0.44, 0.71, and 0.86, anterodistal angle with 1 spine, posterior margin scalloped, with minute spines at 0.12, 0.50, 0.60, 0.72, 0.84, 0.91, and 0.98, posterodistal angle with 1 spine; ischium anterodistal angle with 1 large and 1 smaller spine; merus narrowing distally, anterior margin spined at 0.38 (2), and 0.68 (2), posterior margin spined at 0.39 and 0.66, distal angles with 1 long and 1 smaller spine each; propod anterior margin spined at 0.22 (2), 0.40 (3), 0.57 (2), and 0.79 (2), anterodistal angle with 1 spine, posterior margin spined at 0.22 (2), 0.40 (2), 0.64 (2), and 0.88 (2), posterodistal angle with 3 spines. Pleopods: all present and biramous though short and broad with third the smallest. Pleopod 1: length 0.67 mm; peduncle broad, margins pilose, 2 coupling spines on inner margin; rami of equal length, broad, inner margin of inner ramus pilose proximally. Pleopod 2: narrower and slightly shorter than first, outer margin of peduncle pilose, inner margin with 2 coupling spines; inner ramus slightly shorter than outer. Pleopod 3: length 0.52 mm; peduncle outer margin pilose, inner margin with 2 coupling spines; rami of equal length, segmentation not very obvious. Gills: comparatively small, simple sacs. Uropod 1: moderately long and fine; peduncle with 3 spines dorsally, a large inter-ramal spur extends 0.5 along rami; outer ramus naked dorsally, slightly longer than inner, with 1 long and 2 shorter terminal spines; inner margin with 3 spines dorsally, 2 long and 1 short spine terminally. Uropod 2: (lost in type, description based on male paratypes) peduncle with 3 dorsal spines; outer ramus naked dorsally, with 2 longer and 2 shorter terminal spines; inner ramus with 3 spines dorsally, 1 long, 2 shorter, and 2 very short terminal spines. Uropod 3: uniramate; peduncle with 1 dorsal spine; ramus with 2 terminal spines.

Female: as for male except where specified:

Length 9.12 mm, width 1.94 mm; depth 2.24 mm. Antenna 1: length 1.52 mm, flagellum with 6 segments. Antenna 2: length 4.44 mm, flagellum with 19 segments.

Gnathopod 1: coxal plate ventral margin less rounded than usual, with about 4 large spines; plinthic ridge not well developed, with a few spines; basos broadening distally, anterior margin slightly concave, spined at 0.63 and 0.80, anterodistal angle with 2 spines, posterior margin slightly convex, spined at 0.73, 0.81, and 0.89, posterodistal angle with 2 spines; ischium curved anteriorly, posterior margin convex with 3 spines at posterodistal angle; merus posterior margin smoothly convex, spined at 0.28, 0.48, 0.64, 0.70, 0.79, 0.82, and 0.85; carpus broadening distally, anterior margin spined at 0.44 (2), and 0.66, anterodistal angle with 3 spines, posterior margin produced distally into a small pellucid lobe, with 2 large spines at the posteroproximal angle, 4 large marginal spines, and 2 smaller spines on the mesial face; propod broadening distally, anterior margin convex, stepped, spined at 0.53 (2), and 0.77 (2), anterodistal angle with 3 large spines, posterior margin convex, with 2 submarginal spines and a row of 3 mesial spines, palm convex, 0.5 propod width, with 2 long spines at anterior end, flanked by a row of about 8 spines, palmar angle 108°; dactyl longer than palm, with 2 small spines at base of terminal spine.

Gnathopod 2: coxal plate ventral margin rounded, with about 8 large spines; gill trilobed, anterior lobe large and ellipsoid; basos broadest medially, anterior margin spined at 0.43, 0.55, and 0.68, posterodistal angle with 2 spines; merus long, posterodistal angle with 2 spines, merus produced posterodistally into a pellucid lobe; carpus anterior margin convex, naked, posterior margin produced into a pellucid lobe; propod long, broadening somewhat distally, both margins naked, anterior margin concave, posterior margin convex and produced distally into a lobe which protrudes beyond palmar area, palm very short and angled very acutely, palmar angle 20°; dactyl short, about 1/4 propod width.

Broodplates: long, narrow, setose only distally.

Uropod 1: peduncle with 4 dorsal spines; inner ramus with 4 dorsal spines. Uropod 2: one of the dorsal spines appears like an inter-ramal spur.

Remarks

P.ihurawao is a small, but abundant species, with a pigmentation pattern consisting of a semi-reticulated bright rufous colour outlining prominent yellow dots. This very distinctive pigmentation pattern enables it to distinguished from P.lesliensis, which occurs on the upper slopes of the forested hills in the region, and from the large bodied Makawe hurleyi, which inhabits the surrounding Canterbury and Otago grasslands, the forest margin, and the forest fringe up to a few hundred metres into the forest. Among other distinguishing characteristics are: the short, blunt pilose pleopods, the extremely long inter-ramal spur on uropod 1, and the weak development of the gnathopods in both sexes. It may be readily distinguished from P.tenuis by its short antenna 1 which reach only up to 0.5 the length of the last segment in the peduncle of antenna 2. The sex ratio is heavily biased toward the female sex, there being 7 females, on average, to every male although the ratio varies from place to place being less biased in wetter habitats. The females are small compared with other landhoppers, but the males are smaller still. This may be due to the comparative harshness of the climate in Canterbury habitats where periodic droughts are common. A small-bodied species has a better chance of survival than a large-bodied form because smaller refugia will serve in times of drought. A sex ratio biased to the more biologically valuable sex, the female, could be of value in drought-prone areas. In wetter conditions than those normally occupied by this species a higher proportion of males may be required because the effective search area for receptive females may be smaller, on average, since the female pheromones would not disperse as far in wetter habitats.

P.ihurawao inhabits forested regions, particularly podocarp-hardwood forests, on the foothills of the Southern Alps and in the coastal forests of Otago. It extends from Dunedin in the south to Marlborough in the north. It lives in the rain shadow of the Southern Alps in a region subjected to periodic drought. Its range largely overlaps that of M.hurleyi, which is primarily a grassland species. P.ihurawao has long been mistaken for P.tenuis, which is not surprising considering the great similarity between them. P.tenuis, however, is more definitely reticulated than is P.ihurawao, its antenna 1 reach further along antenna 2, and its pleopods are narrower with the third pair much smaller. Sexually differentiated males are common in P.tenuis populations, but are uncommon in P.ihurawao populations. The two species show marked similarities in the pilosity of the pleopods and in the general shape and length of the appendages. It seems probable that P.ihurawao is a comparatively recent off-shoot from the P.tenuis stock which became adapted to somewhat drier conditions that those normally occupied by P.tenuis; although it should be noted that P. tenuis inhabits analagous forests on the east coast of North Island where periodic droughts are also frequent.

The isolating mechanism that caused the speciation of P.ihurawao from P.tenuis could well have been the constriction of range of both into separate refugia during periods of cold climates and ice ages. Alternatively, the rain shadow of the Southern Alps becomes drier inland from the regions occupied by P.ihurawao. No landhoppers are found in these arid central basins, so that gene flow from east to west is broken. The alpine barrens of the Southern Alps may constitute an isolating barrier, but landhoppers can reach well above bush line, and generally the same species occurs on both sides of a mountain chain. So mountains are not as effect as barriers as are arid regions. Gene flow might be maintained around the southern coast, but such a flow would often be interrupted by severe climatic events, such as glaciations, and the populations would be competing in suboptimal habitats with better adapted coastal species. Certainly the arid zone is probably a much more ancient barrier than the Pleistocene glaciations, so is the more likely isolating mechanism.

The early state of development of the eggs in the broods of the ovigerous females collected in the Hapuku Reserve on 30/VIII/1981 indicate that breeding commences in the spring. The broods carried by these females were very small and consisted only of 2, 3 or 4 eggs depending on the size of the female. Other collections indicate that the species does not breed in winter but the gills do not seem to change in form or size as do those of M.hurleyi in winter.

This species shows considerable morphometric variation from place to place. For example, those from the Dunedin district are much larger and have a first antenna which extends just beyond the joint of peduncle segments 4 and 5 of antenna 2. The pigmentation pattern of these specimens is somewhat characteristic of the region. I regard these as no more than subspecific differences in a species whose gene pool has undergone frequent and prolonged disruption by being isolated into mesic islands on hills and mountains separated by arid valleys. But it may be that there is a species swarm consisting of a number of very similar sibling species derived from the same parental stock, each isolated region having given rise to its own specific form. Thus those in the Kaikoura district may be specifically different from those in the vicinity of the Peel

Forest, and these may be different again from the forms around Dunedin. The resolution of this problem would require a great amount of work and very sophisticated techniques and so lies beyond the scope of the present study. I have used the smaller Peel Forest specimens for the types rather than the larger Dunedin ones (maximum measured sizes: male 15.3 mm, female 15.5 mm body length) because Peel Forest lies in the middle of the species' range whereas Dunedin is at its known southern limit.

Parorchestia longicornis (Stephensen), 1938 in part.

Figures 345 to 353

Orchestia tenuis Hurley, 1957: 166-172.

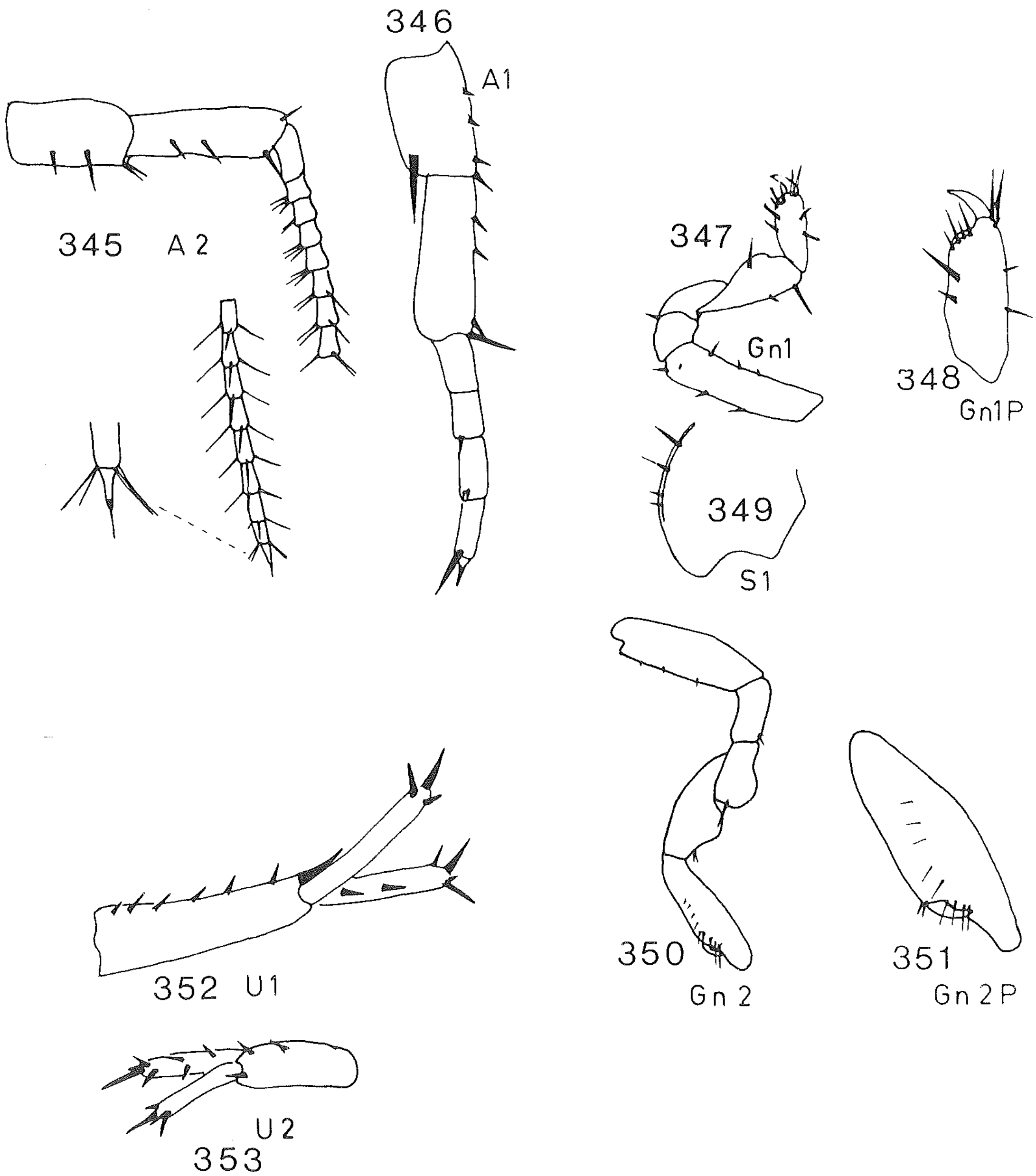
Holotype: female: Stewart Island, under logs and stones, in the forest at great altitudes, 21/XI/1914, Th.Mortensen.

New material: male: Halfmoon Bay, Stewart Island, R.R.Forster, 21.XI.1946, in leaf mould with 2 females and 6 individuals of *P.tenuis*.

Description of male:

Length: 7.17 mm, width 1.23 mm, depth 1.37 mm. Antenna 1 compressed dorsoventrally, length 0.96 mm, extends to 0.66 along the last segment of the antenna 2 peduncle; peduncle segment 2 inner margin with 3 spines, inner distal angle with 1 spine, outer distal angle with 1 large spine; segment 2 length 1.36 that of segment 2, narrower than segment 2, broadening distally, inner margin with 2 spines, inner distal angle with 1 spine, 1 long spine on superodistal margin, outer margin naked; flagellum of 5 podomere segments, each podomere successively longer and narrower except the last which is short, triangular, and bears a short, close-bound terminal tuft.

Antenna 2: length 4.81 mm; peduncle segment 4 superior margin naked, inferior margin with 2 large spines, inferodistal angle with 2 spines; segment 5 superior margin naked, inferior margin with 2 spines, inferodistal angle with 1 long spine; flagellum of 36



FIGURES 345-353. Parorchestia longicornis. 345, antenna 2. 346, antenna 1. 347, gnathopod 1. 348, gnathopod 1 propod. 349, coxal plate 1. 350, gnathopod 2. 351, gnathopod 2 propod. 352, uropod 1. 353, uropod 2.

podomere segments, each quite constricted proximally and bearing a long, fine spine distally, scarcely tapering distally, terminal segment margins concave, with a long, fine terminal spine. Mouthparts: Upper lip: wider than deep, ventral margin with a greater radius of curvature than usual, sparsely pilose, inner shelf present. Mandible: molar 14-striate, molar medial seta present. Maxilla 1: outer plate has a minute palp on outer margin. Maxilla 2: outer plate distal margin rounded with row of inwardly curved spines, outer margin naked; inner plate foliaceous, distal margin with row of inwardly curved spines terminating on inner margin with stout pilose seta. Maxilliped: not broad, spine teeth on inner plate longer than usual, palp segment 4 present, not large, but not obscured by segment 3.

Gnathopod 1: coxal plate ventral margin rounded and with long spines; basos broadening distally, curved anteriorly, anterior margin concave, spined at 0.38, 0.53, and 0.76, posterior margin slightly scalloped, spined at 0.15, 0.29, and 0.58, posterodistal angle with 2 spines; carpus anterior margin spined at 0.66, anterodistal angle with 2 spines, posterior margin produced into a pellucid lobe medially; propod broadening to 0.3 then narrowing distally, palm transverse, length 0.5 propod width, well defined by sclerotic area and flanked by long spines; dactyl stout, projects slightly beyond propod margin when occluded.

Gnathopod 2: much as for female: basos anterior margin spined at 0.28, 0.42, and 0.65; ischium and carpus posterior margins produced into large pellucid lobes; propod mitten-shaped, palm small, oblique.

Peraeopod 1: segment margins with comparatively large spines; basos curved anteriorly, anterior margin slightly stepped, spined at 0.37, 0.52, 0.73, and 0.87, posterior margin spined at 0.17, 0.42, and 0.65; merus broadening distally but less than is usual, anterior margin spined at 0.28 and 0.48, anterodistal angle with 1 spine; posterior margin spined at 0.25, 0.49, and 0.56, posterodistal angle with 2 spines; carpus anterior margin naked, anterodistal angle with 2 spines, posterior margin scalloped, spined at 0.23, 0.40, and 0.68, posterodistal angle with 1 spine; propod curved slightly posteriorly, narrowing slightly distally, length 1.1 carpus length, anterior margin stepped, spined at 0.35, and 0.77 (2), posterior margin spined at 0.24 (1), 0.36 (2), 0.60 (2), and 0.80 (2).

Peraeopod 2: basos curved anteriorly, broadening distally, anterior margin with large spines at 0.76 and 0.87, posterior margin spined at 0.24, 0.36, 0.60, and 0.80, posterodistal angle with 1 spine; ischium posterodistal angle with 1 spine; merus anterior margin spined at 0.51, anterodistal angle with 1 spine, posterior margin spined at 0.27 and 0.53, posterodistal angle with 1 spine; carpus shorter and narrower than merus, anterior margin naked, anterodistal angle with 1 spine, posterior margin spined at 0.41, 0.74, and 0.88, posterodistal angle with 2 spines; carpus narrowing distally, anterior margin spined at 0.38 and 0.73, anterodistal angle with 1 spine, posterior margin spined at 0.32, 0.55, and 0.77.

Peraeopod 3: coxal plate lobes with only 1 or 2 spines; gill simple; basos an inverted pyriform shape, anterior margin slightly scalloped, nearly straight, spined at 0.25, 0.48, and 0.77, anterodistal angle with 2 spines, posterior margin stepped, spined at 0.32, 0.57, 0.78, and 0.92; ischium anterior margin nearly straight, anterodistal angle with 2 spines; merus broadening distally, anterior margin scalloped and stepped, spined at 0.24 (1), 0.46 (2), and 0.88 (1), anterodistal angle with 1 long spine, posterior margin stepped, spined at 0.44, posterodistal angle with 2 long spines; carpus 1.15 length merus, anterior margin deeply scalloped, spined at 0.34 (2), 0.57 (2), 0.78 (1), and 0.92 (1), posterior margin naked, posterodistal angle with 2 spines; propod narrowing slightly distally, both margins stepped, anterior margin spined at 0.24 (1), 0.35 (2), 0.56 (2), and 0.77 (2), posterior margin spined at 0.40 (2), and 0.73 (2), posterodistal angle with 2 spines.

Peraeopod 4: basos ovoid, both margins slightly scalloped, anterior margin spined at 0.38, 0.57, 0.76, and 0.98, anterodistal angle with 1 spine, posterior margin spined at 0.05, 0.20, 0.37, 0.60, and 0.77; ischium anterodistal angle with 2 small spine; merus broadening distally, both margins scalloped, anterior margin spined at 0.28 (2), 0.53 (2), and 0.80 (1), anterodistal angle with 3 spines, posterior margin spined at 0.27 and 0.49, posterodistal angle with 2 spines; carpus, both margins stepped, anterior margin spined at 0.19 (1), 0.32 (2), 0.56 (3), and 0.91 (2), anterodistal angle with 1 spine, posterior margin spined at 0.46 (1), and 0.68 (2), posterodistal angle with 3 spines; propod damaged.

Peraeopod 5: basos subtriangular with convexly rounded margins, anterior margin with large spines, posterior margin has minute spines; ischium anterodistal angle with 1 long and 1 small spine; merus margins subparallel, long, anterior margin scalloped, spined at 0.13 (1), 0.28 (2), 0.58 (2), and 0.89 (2), anterodistal angle with 3 spines, posterior margin spined at 0.33 and 0.57, posterodistal angle with 3 spines; carpus narrower than and only slightly longer than merus, margins subparallel, stepped, anterior margin spined at 0.32 (2), 0.54 (1), 0.75 (1), and 0.88 (3), posterior margin spined at 0.43 and 0.68, posterodistal angle with 3 spines; propod length 1.38 carpus length, narrowing distally, margins stepped, anterior margin spined at 0.15 (1), 0.25 (2), 0.45 (2), 0.71 (2), and 0.85 (2), posterior margin spined at 0.29 (2), 0.52 (2), 0.72 (1), and 0.89 (2), posterodistal angle with 1 spine.

Pleopods: lengths, 1 = 0.76 mm, 2 = 0.61 mm, 3 = 0.52 mm; all very broad with short stout peduncles bearing setae on the outer margin of the third and a pair of coupling spines on the inner distal angle of each; rami: outer much longer than inner (nearly twice), segmentation obscure on all rami, marginal setae dense and of even length throughout.

Uropod 1: peduncle longer than rami, with 6 dorsal spines, a large inter-ramal spur is present reaching 0.38 along rami; outer ramus naked dorsally, with 3 long and 2 short terminal spines; inner ramus as long as outer, with 2 dorsal spines and 2 long and 2 short terminal spines. Uropod 2: peduncle with 3 spines dorsally; outer ramus naked dorsally; inner ramus with 2 rows of 2 dorsal spines, one row on outer margin, the other on the inner margin; both rami terminate with 2 large and 2 small spines.

Remarks

In 1938 Stephensen described a new species, *Parorchestia stewarti*, as having two forms: *brevicornis* with short antennae 2, and *longicornis* with long antennae 2. Unfortunately, he was able to describe only the females of both forms. Hurley (1957) merged the species into *Orchestia tenuis*. I agree with this decision with respect to *brevicornis*, given the present state of knowledge, but obviously *longicornis* is a good species.

P.longicornis is clearly differentiated by its long antenna 2 and the broad, short pleopods. The double row of spines on the dorsal margin of the inner ramus of uropod 2 is present on all the specimens (male and female) I have examined but was not figured by Stephensen.

This is a species with a sex ratio heavily biased toward the female sex. In the 312 collections of Stewart Island material I have examined I have found only one male, the one described herein. Probably, this is because males are much smaller than females; collectors tend to collect larger specimens and thus males, if they are smaller as is common in landhoppers, tend to be under-represented in collections.

Genus Talorchestia Dana, 1852

Stebbing, 1906:543. Chilton, 1917:293. Shoemaker, 1942:187. Reid, 1947: 15. Hurley, 1956:359. Shyamasundari, 1971:30-31.

Remarks

One of the most important characters used in separating *Talorchestia* from '*Orchestia*' is the female gnathopod 1, which in *Talorchestia* is simple while in *Orchestia* it is chelate. But the female gnathopods may be intermediate in form between simple and chelate. Shoemaker (1942), Reid (1947) and Hurley (1956) have discussed this difficulty. In an attempt to find more realistic criteria Chilton (1921) and Shyamasundari (1971) drew attention to differences in the male second gnathopod between the two genera. In particular, Shyamasundari noted that *T.martensii* and *Orchestia platensis* differ in that *T.martensii* has two rows of spines on the palm border of the propod of the male gnathopod 2 whereas in *O.platensis* only a single row of spines is present. Unfortunately, in the New Zealand specimens of terrestrial *Talorchestia*, this distinction breaks down since *T.patersoni* and *T.aotearoa*, the only truly terrestrial *Talorchestia* in New Zealand, both have a single, though dense, row of spines on the palmar margin. If this criterion of a double spine row designating *Talorchestia* is to be adopted strictly, then these two New Zealand species would be excluded from the genus. Yet I believe that they do not belong to the '*Orchestia*' complex because although they are more spiny (a plesiomorphic feature) than are other landhoppers, they show a number of apomorphic features. Thus they must have had a separate origin from the rest of the New

Zealand landhoppers and more properly belong to Talorchestia.

The weakness of Shyamasundari's criterion can be shown in the New Zealand supralittoral Talorchestia where only the oceanic beach forms T.cookii, tumida, spadix and older males of quoyana) have the double row of spines. Those species found more inland or in places exposed to a fresh water influence (telluris, chathemensis?, dentata?) do not have the double spine row. Thus the presence or absence of a double spine row is an adaptive character associated with species inhabiting the physically demanding oceanic supralittoral environments, and of no value in generic separation.

Shyamasundari (1971) also reported a difference in neurosecretory cells between T.martensii and O.platensis. I have not tested the New Zealand species of Talorchestia and the 'Orchestia' complex for this character. He also mentioned that all the truly terrestrial species are Orchestia while the supralittoral species are Talorchestia. The present work indicates that this is not so. It is true that light-bodied, lightly spined forms are terrestrial while the robust-bodied, heavily spined forms are mainly supralittoral, but this is a consequence of the difference between the terrestrial and supralittoral environments.

Characters which may have some value in separating Talorchestia from 'Orchestia' are as follows:

- In Talorchestia the male gnathopod 1 palm is formed by the posterior margin becoming produced, especially distally. Here there is an absence of the very marked palmar sclerotic area seen in members of the '*Orchestia*' complex. In young *Talorchestia* males and the more terrestrial species of *Talorchestia* this posteriad extension may not be so marked, so that the first gnathopod appears to be simple or almost so. This is not seen in the members of the '*Orchestia*' complex that I have examined.

– The male second gnathopod usually has a finger which is guided and protected distally by a lobe at the posterodistal end of the palm. However, the very terrestrial species *T.aotearoa* does not have this because its second gnathopods in the male are feminized or juvenile in form.

It may not be possible to have absolute criteria for the separation of landhopper genera. In fact, if the aim is to show phylogenetic relationships it may be a positive hindrance to search for absolute criteria in such an evolutionary labile group of organisms where it is apparent that much parallel and even convergent evolution has occurred. The difficulty in placing apomorphic, sexually similar species in appropriate genera may be more apparent than real since the supralittoral members of the '*Talorchestia*' and '*Orchestia*' complexes can readily be distinguished using traditional criteria. From that point the relationships of the more terrestrial species can be unravelled.

Talorchestia patersoni Stephensen, 1938.

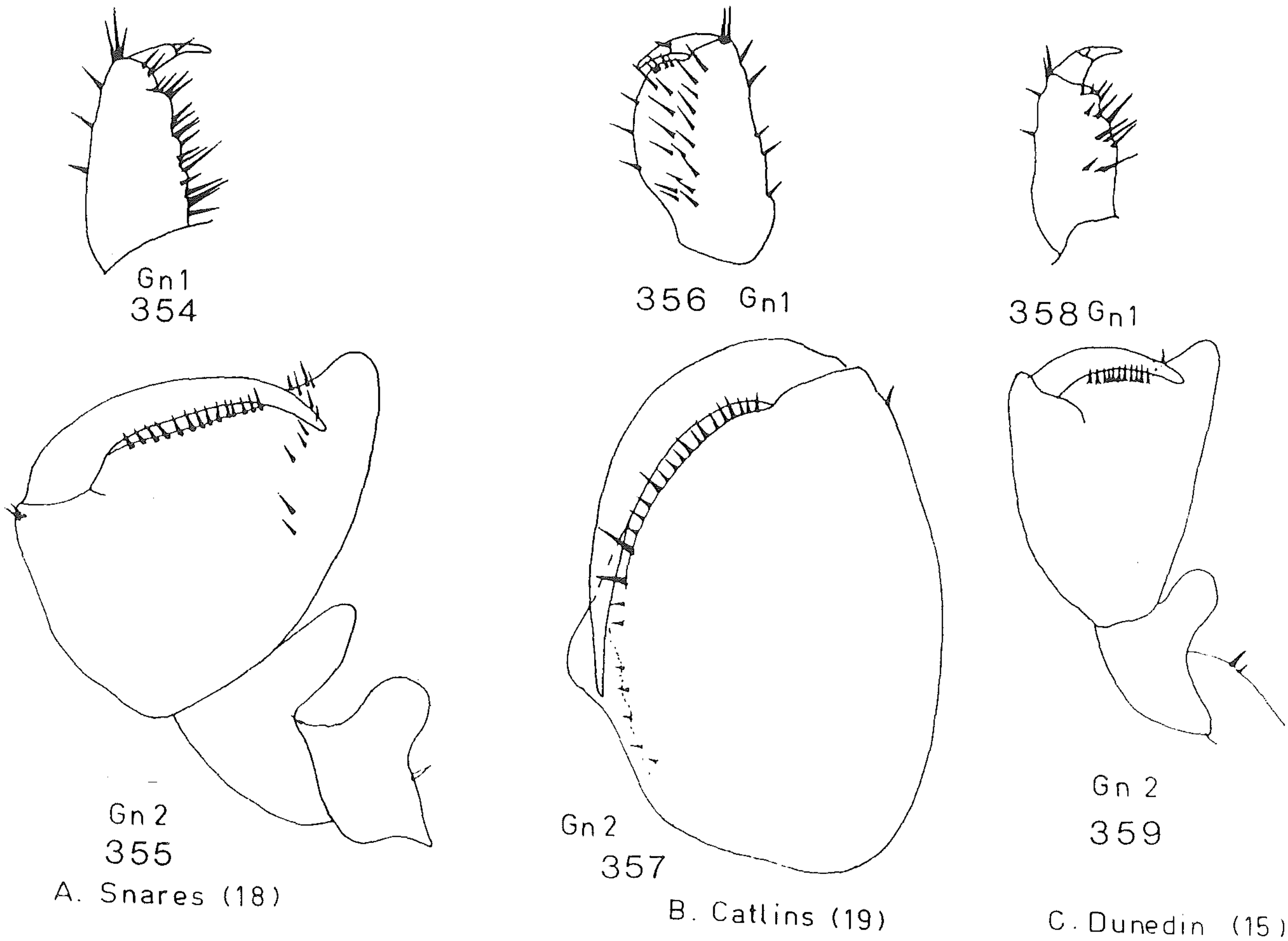
Figures 354 to 360

Talorchestia patersoni Stephensen, 1938.

Orchestia patersoni Hurley, 1957, p.196-198.

Localities and collectors:

Paterson Bay, Stewart Island, Th.Mortensen, 21/XI/1914, under rocks or stones, forest, at great heights. Snares Island, R.A.Falla, -/XII/1947, leafmould. Snares Island, D.S.Horning, -/III/1971. Bench Island, A.J.Lindsay, 9/VII/1948. Stewart Island, R.R.Forster, 20/XI/1946, in garden leafmould. Solander Island, R.A.Falla, 4/XII/1947, leafmould. Town Belt, Dunedin, K.W.D., 26/V/1967, ex cut-over podocarp-hardwood forest leaf litter. King St., Dunedin, 26/V/1967, K.W.D., in long grass litter in a suburban garden taken with *Makawe hurleyi*. Sealers Bay, Codfish Island, (off Stewart Island), R.K.D., 8/XI/1948, under *Phormium*. Lords River, S.E.Stewart Island, 47°07'S 168°08'E, R.K.D., B.A.H., 29/I/1955, in *Senecio* scrub litter. Nelly Island (off Stewart Island), 47°12'S 167°42'E, R.K.D. and B.A.H., 22/I/1955, taken with *Kanikania motuensis* in leafmould. Owens Island (off S.E.Stewart Island), R.K.D. and B.A.H., 29/I/1955. Hidden Island (off S.W.Stewart Island), R.K.D. and B.A.H., 28/I/1955, in leafmould with *K.motuensis*. Bench Island, Foveaux Straight, C.J.L., no date. Solander Island, R.A.F., 9/XII/1947. Crooked Reach, Port Pegasus, Stewart Island, R.K.D., 22/I/1955, with *P.tenuis*. S.W.Stewart Island, R.K.D., 28/I/1955, with *P.tenuis*. Owens Island, (off



FIGURES 354-359. Talorchestia patersoni gnathopod 1 & 2. 354, gnathopod 1 Snares Island specimen. 355, gnathopod 2 Snares Island specimen. 356, gnathopod 1 Catlins specimen. 357, gnathopod 2 Catlins specimen. 358, gnathopod 1 Dunedin specimen. 359, gnathopod 2 Dunedin specimen.

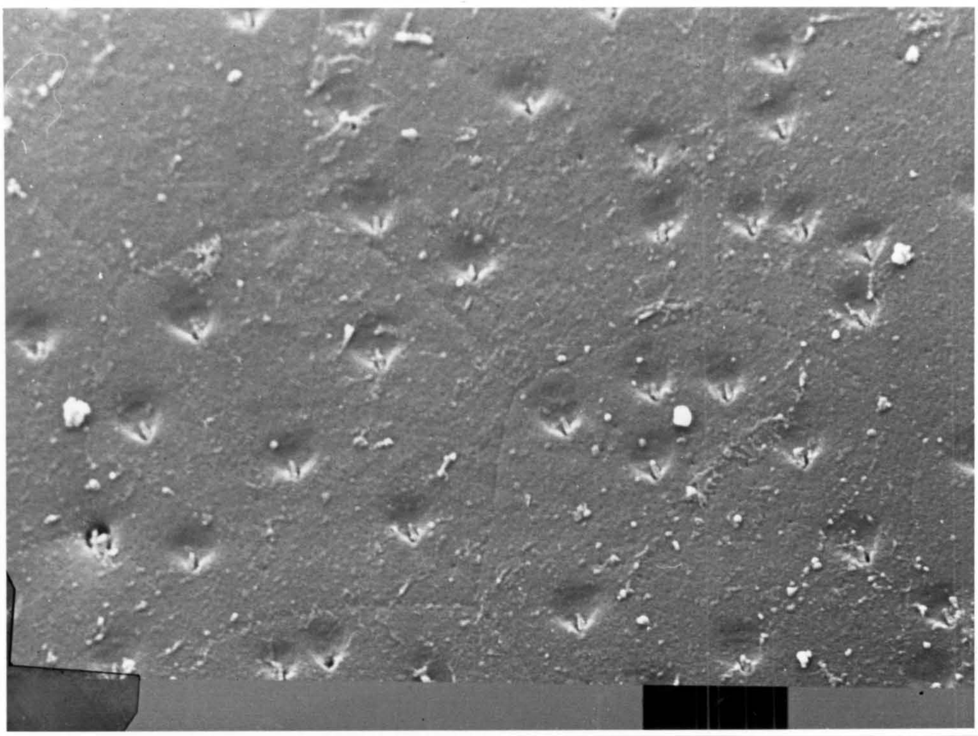


FIGURE 360. Cuticular structure of *Talorchestia patersoni*. Macropores are scattered over the surface at a density of 76 per square millimetre, and the ducts of some are obscured by spheres of mucoid material. The cuticular polygons measure on average of 11 x 10.6 micrometres.

S.E.Stewart Island), R.K.D., and B.A.H., 29/I/1955. Opoho Bush, Dunedin, C.L.W., 10/XII/1970, taken with *M.hurleyi*, and *P.ihurawao*. Kundy Island (off S.E.Stewart Island), R.K.Dell, 21/V/1956, taken with *P.tenuis* and *K.motuensis*. Solomans Island (*sic*) (off S.W.Stewart Island), R.K.Dell and B.A.Holloway, 25/I/1955, with *K.improvisa*. N.Entrance, Lords River, S.E.Stewart Island, R.K.Dell and B.A.Holloway, 29/I/1955, *Senecio* leafmould. Mokinui Island (off S.W.Stewart Island), R.K.Dell and B.A.Holloway, 28/I/1955, with *K.motuensis*. Ulva Island, Paterson Inlet, Stewart I., L.C.C. and N.A.D., 16/XI/1981, in podocarp leaf litter with *P.tenuis* . Rodrigues Tr., Codfish Island, L.C.C. and N.A.D., 6/I/1982, in *Myrsine* leaf litter. Warren St., Reserve, Oamaru, K.W.D., 6/V/1983, under *Phormium* taken with *M.hurleyi*. *P.ihurawao*, and *M.otamatuaheke*. Waipati Beach, 38 km S.W. of Owaka, Catlins district, Southland, G.Kuschel, 15/I/1978, in litter and rotten wood. Purakaunui Falls, 15 km S.W. of Owaka, Otago, G.Kuschel, 15/I/1975, sifted litter and rotten wood.

Remarks

Stephensen (1938) placed this species in *Talorchestia* because the female has a simple first gnathopod and the male has a chelate gnathopod with an oblique palm and a strongly chelate second gnathopod. He pointed out, however, that it is very different from the other three New Zealand species of *Talorchestia* known at that time. Hurley (1957) did not believe that it belonged in *Talorchestia* and so placed it in *Orchestia* on the grounds that the palm on the male first gnathopod is not well defined, especially in specimens from Snares Island, and that the second peraeopod does not show the heavy spur and notching on the dactylos which is characteristic of *Talorchestia*. He observed that it is much like the terrestrial *'Orchestia'*, and because he considered the simple male gnathopod in the Snares Island specimens to link the species with *Orchestia*, he felt justified in including it in *Orchestia*. This argument is difficult to follow since his own definition of *Orchestia* states: "Like *Talitrus* except that gnathopod 1 in male and female is less strongly developed and subchelate instead of simple; ...". Obviously, this species does not belong in *Orchestia*.

Further evidence against its inclusion in *Orchestia* is that it is far more 'spiny' than is a typical landhopper, especially on its gnathopods. If it is included in the evolutionary line leading to *Parorchestia tenuis*, then it fits near that species as an advanced terrestrial species because of its apomorphic features, particularly its reduced pleopods. Yet it is a strand-coastal species, which never penetrates far inland. Physiological evidence presented in Part II, in the section on osmotic and ionic relations, shows that it is not as terrestrial as *M.hurleyi*, a coastal species, and, therefore, is far less terrestrial than the inland *P.tenuis*. Its body pattern resembles *P.tenuis* in being reticulated, but there are many differences, which may be fundamental, in the way in which the reticulation is achieved. In addition, the colours, and thus probably the chemical nature, of the pigments differ. Furthermore, the surface structure of its cuticle is very different from that of

P. tenuis.

It may be argued that loss of pleopods relates it to the Parorchestia group. Yet no other member of the Parorchestia group has completely vestigial pleopods, because at least the first pair of pleopods retains the function of agitating the water surrounding the gills. Total loss would seem to be disadvantageous and in fact only occurs in two species world-wide. It is as though this species belongs to an assemblage which has not been able to adjust the development rate of individual pleopod pairs as has every other group of landhoppers. Instead of reducing one or both of the last pairs it has reduced all, probably thereby gaining the advantage of smaller, reduced pleopods but incurring the penalty of having none. Viewed this way, the position of this species is much easier to determine. It belongs to an assemblage different from that of the "Orchestia-Parorchestia" group of species, which has made an independent incursion into the terrestrial environment with a slightly different, although largely parallel, set of adaptations. But to which group does it belong?

I believe that Stephensen was correct in his original placement: the species belongs in Talorchestia. The Stewart Island and South Island specimens are good Talorchestia except for the fineness or delicateness of the body, which probably accounts for the weak spur on the peraeopod 2 dactyl. The antenna 2 are short, stout, and 'triangular', the male gnathopod 1 propod of fully mature specimens is chelate and bears the extension of the posterior margin seen in many _Talorchestia_ species, the male propod of gnathopod 2 looks typically _Talorchestia_-like even to the pellucid lobe at the posterior end of the palmar region, and the body is spiny. That it has a delicate body and not a robust one does not, in my opinion, argue against its inclusion in _Talorchestia_. A fine, delicate body is a significant terrestrial adaptation allowing fuller utilization of litter and soil spaces and refugia in a physically stable environment. The robust body of the supralittoral species, on the other hand, is an adaptation to the physically rough, harsh, and unstable environment of the seashore.

Snares Island specimens:

The Snares Island specimens are different from those of Stewart Island and South Island in that they possess a relatively simple gnathopod 1 in the adult male, a smaller body, and a different male gnathopod 2. The simple gnathopod 1 in the adult male represents a modification of the _Talorchestia_-like condition seen in the Stewart Island and South Island specimens and does not, in may opinion, link the species to _Orchestia_ as believed by Hurley. Fully mature Snares Island males resemble young adult South Island/Stewart Island forms. Figures 354 to 359 shows the fully mature male propods on gnathopods 1 and 2 of adult instar 6 from the Catlins (South Island), adult instar 2 from Dunedin (South Island), and adult instar 5 from Snares Island. The figure shows that the old male from the Snares resembles the young male from Dunedin. 'Chelateness' is a secondary sexual characteristic, so it is obvious that neoteny is involved here, and that the Snares population represents a more neotenous population of _T.patersoni_. Neoteny is a common mechanism in landhopper evolution. It is clearly seen in _M.hurleyi_ which is typical of the many species in which males closely resemble females. In such species, the adaptive advantage of fine, delicate bodies renders the copulatory carrying of females by males difficult or impossible. Thus secondary sexual characteristics become redundant or even disadvantageous because they are cumbersome. Evolution has proceeded by a reduction or switching off of the rate genes controlling development of the secondary sexual characters and some other redundant parts such as the second and third pleopods, or the spines on the uropods.

The differences between the Snares Island and the other populations of _T.patersoni_ represent profound alterations to the gene pool, so do the Snares specimens belonging to _T.patersoni_? They are very similar, but that may be due to strictures of the terrestrial environment enforcing a certain degree of similarity. Hurley suggested that they might be a different subspecies. I suggest that they may even be different species.

Atkinson and Bell (1973) stated that endemism is strong on the subantarctic islands amongst both animals and plants. Of the other landhopper species present on the Island, _Tara simularis_ and _K.improvisa_ are endemic while only _P.tenuis_ is not, and upon further investigation, even this latter species will probably turn out to be at least subspecifically different. So the Snares population may be a separate species but in the absence of more complete criteria for species separation, it is probably better to designate the two populations as subspecies: the northern one as *T.patersoni patersoni* and the Snares Island population as *T.patersoni snaresi*. Stephensen's description is of the larger-bodied population on Stewart Island which serves as a description of the South Island specimens as well, while Hurley's is mainly of the small-bodied *snaresi* on Snares Island.

Talorchestia aotearoa new species

Figures 361 to 392.

Types:

The holotype male was collected at Castle Hill (E.Alfredton), North Island, New Zealand, $40^{\circ}40'$S, $175^{\circ}55'$E, by myself, and has been deposited in the Canterbury Museum. An allotype female was taken at the same locality and has also been deposited in the Canterbury Museum. Paratypes have been deposited in the National Museum, Wellington, the Auckland Museum, and the Entomology Division of the DSIR, Auckland.

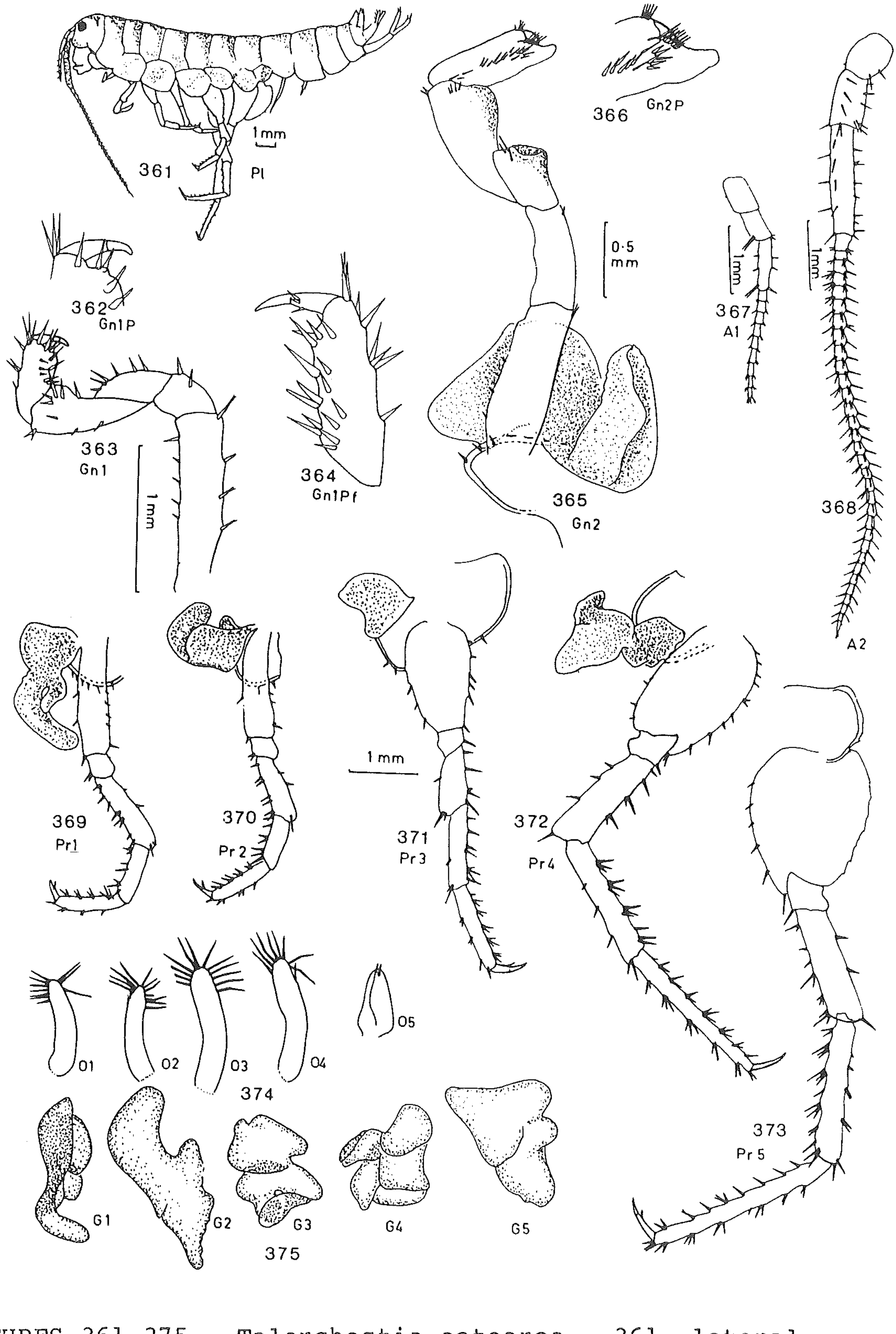
Localities (Fig.391):

Throughout the North Island from sea level to at least 1000 m. Western Marlborough, Nelson, and the West Coast of the South Island straggling to Fiordland and Stewart Island. Abundant on Kapiti Island, Blumine Island, D'Urville Island, Chetwode Islands, Maud Island, and Stephens Island. Its peak density is in coastal regions.

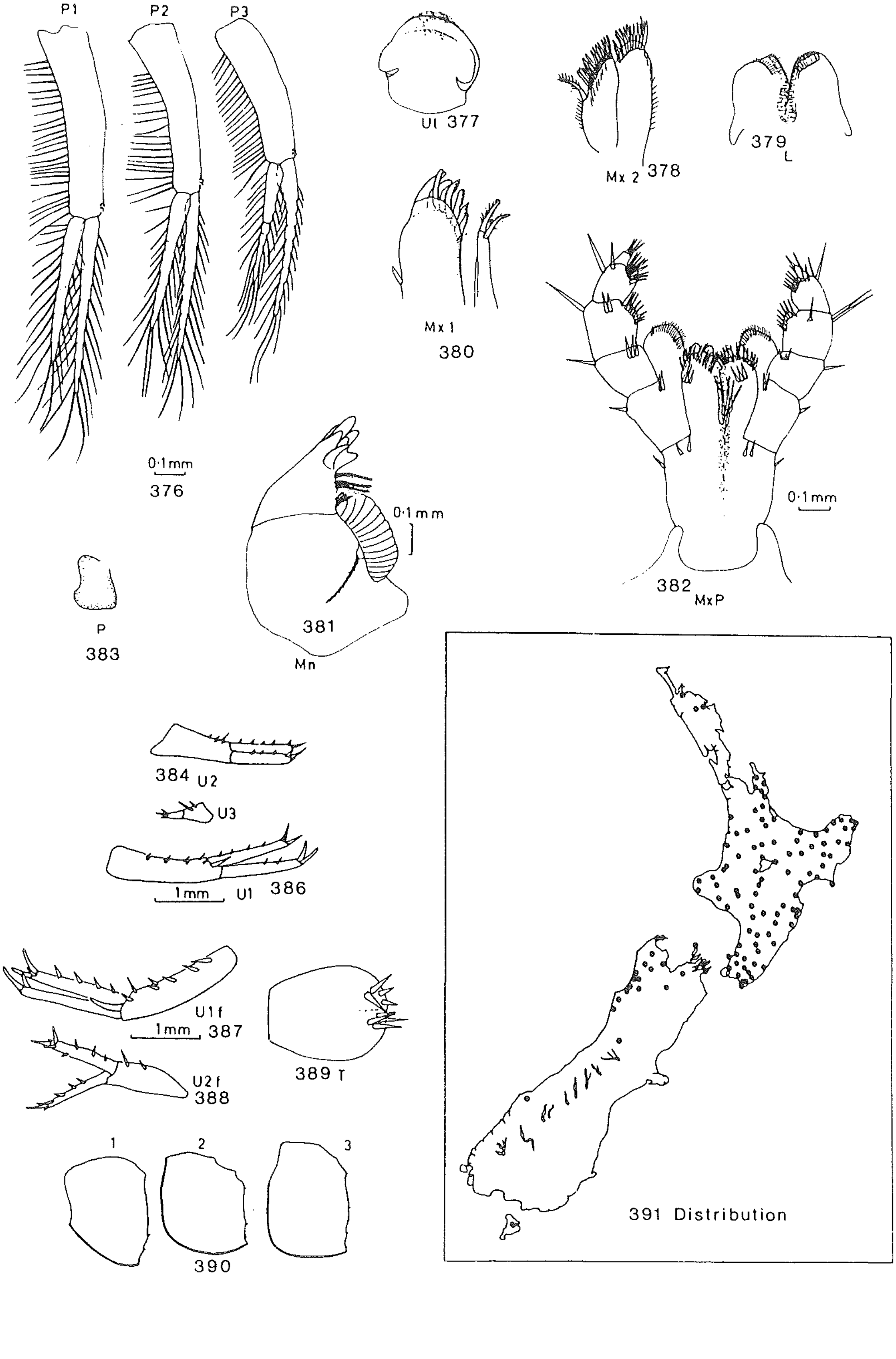
Etymology: named after the Maori name for New Zealand, which has a number of possible meanings, but is usually assumed to mean "Land of the long white cloud"(Reed and Brougham, 1978).

Diagnosis:

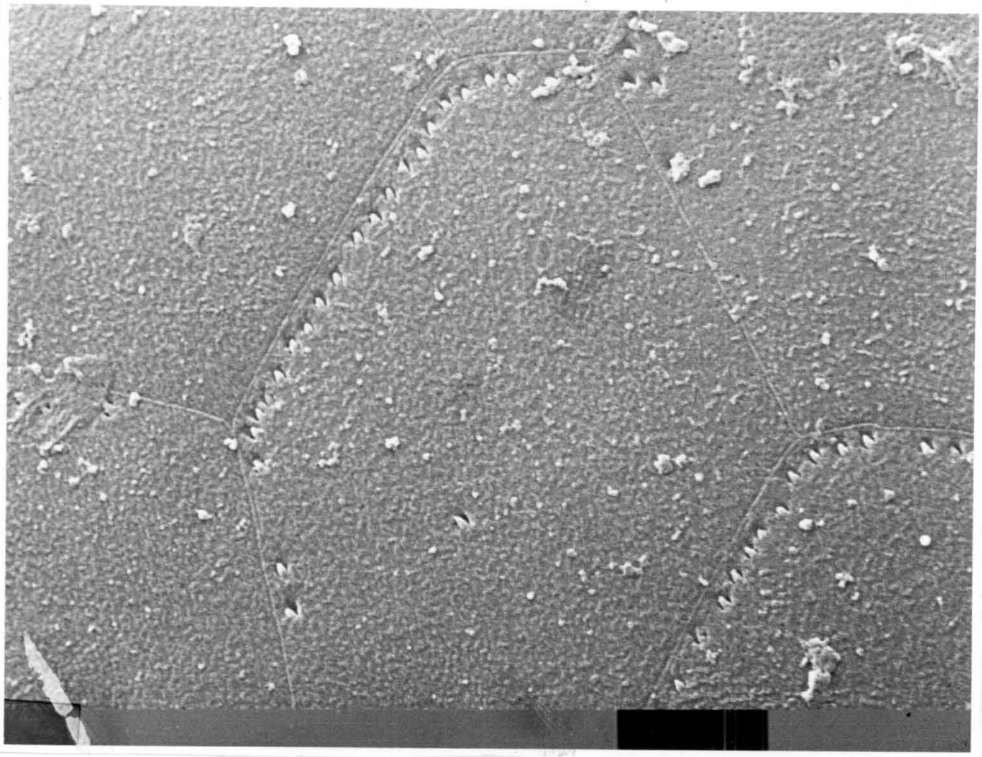
A large, weakly sexually dimorphic landhopper, of the genus *Talorchestia*, with large eyes (0.33 length of head), antennae 1



FIGURES 361-375. <u>Talorchestia</u> <u>aotearoa</u>. 361, lateral aspect. 362, gnathopod 1 male propod. 363, gnathopod 1 male. 364, gnathopod 1 female propod. 365, gnathopd 2 male. 366, gnathopod 2 male propod. 367, antenna 1. 368, antenna 2. 369, peraeopod 1. 370, peraeopod 2. 371, peraeopod 3. 372, peraeopod 4. 373, peraeopod 5. 374, oostegites. 375, gills.



FIGURES 376-391. Talorchestia aotearoa. 376, pleopods 1,2 &3. 377, upper lip. 378, maxilla 2. 379, lower lip. 380, maxilla 1. 381, mandible. 382, maxilliped. 383, penal plate. 384, uropod 2. 385, uropod 3. 386, uropod 1 male. 387, uropod 1 female. 388, uropod 2 female. 389, telson. 390, epimeral plates. 391, distribution.



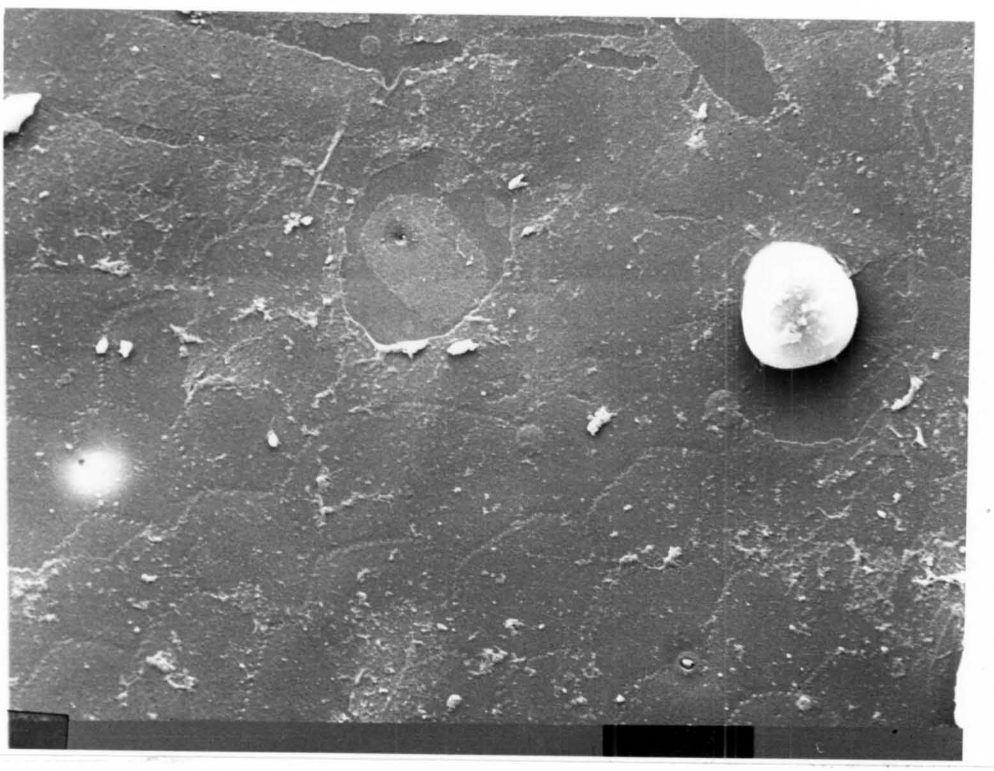


FIGURE 392. Cuticular structure of Talorchestia aotearoa abdominal segment 2 (midlateral). Mesopores are scattered over the body surface and arranged in arcs or lines at the posterior borders of the cuticular polygons. Each pore has a structure resembling a 'veranda'. The scale bar indicates 4 micrometres. The lower micrograph shows macropores opening into dermal cell polygons. Much mucoid material is present. The scale bar indicates 20 micrometres.

comparatively long, reaching almost to the end of antenna 2 peduncle; antenna 2 long (2/3 length of body) and slender; gnathopod 1 weakly subchelate in male, simple in female; gnathopod 1 propod very spiny in both sexes; gnathopod 2 mitten-shaped in both sexes; gills moderately large and multilobed; pleopods slender, all present and biramous, the third pair smaller than the other two; uropod 1 outer ramus naked in females and younger males, spined in older males, pigmentation of the hooped type.

Description:

Male:

Length 13.9 mm, width 3.4 mm, depth 3.8 mm. Body moderately deep. Pigmentation: in life, rufous with a glistening, irridescent surface in alcohol, each segment with a diffusely-edged hoop of rose pink on a white-cream background; antennae suffused with pink; sideplates with diffuse pink patches. Eye round, very black, about 0.33 head length. Antenna 1: length 3.4 mm, almost as long as antenna 2 peduncle; peduncle segment 1 with very small spines at superior and inferior distal margin; peduncle segment 2 narrower and slightly shorter than segment 1, with a pair of long spines near inferodistal angle, a small spine at superodistal angle; segment 3 nearly twice as long as segment 2 but narrower, spines at 0.38 and 0.55 on superior margin, and at 0.35 and 0.57 on inferior margin, double spines at superior and inferior distal angles; flagellum of 10 podomere segments, each podomere except the last 2 with double spines at superior and inferior distal angles; penultimate podomere has a strong tuft of 3-4 spines on inferodistal angle; terminal segment has a terminal tuft of very few spines. Antenna 2: length 9.0 mm, slender and moderately long; peduncle segment 3 has both margins convex, with one large and one small spine at superodistal angle, inferior margin with 2 stronger spines, inferodistal angle with a group of 2-3 stout spines; segment 4 is longer than segment 3, with slightly sinuous margins, dorsal margin naked, lateral margin with an axial row of 3 spines, ventral margin with spines at 0.38 (1), 0.55 (1), 0.77 (2), and 0.85 (1), superodistal angle with 1 spine, lateral distal margin with 2 strong spines, and inferodistal angle with 2 spines; segment 5 longer than segments 3 and 4 combined, narrowing slightly distally, superior margin with 3 spines, lateral margin with 4 spines, inferior margin with spines at 0.25, 0.35 (2), 0.53, 0.66 (2), 0.81, 0.87, and 0.95 (2), superodistal angle has 1 spine, inferodistal angle has 2 spines; flagellum moderately long and slender with 32 podomere segments, each podomere has groups of 2 long, slender spines at each of the 4 distal angles, terminal segment long with a short tuft of 8-10 spines terminally. Mouthparts. Upper lip: lateral margins a little expanded and pilose, ventral margins heavily pilose. Left mandible: with 6 cuspate incisor, lacinia mobilis 4-toothed, 4 inter-dentate pilose setae, admolar setal tuft not obvious, molar 19-striate, molar medial seta absent. Right mandible: with a 5-cuspate incisor, postmolar setal tuft prominent, molar medial seta prominent, length about 0.5 width of mandible, heavily pilose. Lower lip: of normal bifid scroll shape, with ventral and inner margins sclerotised and pilose with 2 rows of fine setae. Maxilla 1: inner plate slender, narrowing distally, with 2 terminal setae heavily pilose; outer plate broader, inner margin nearly straight, sparsely pilose, outer margin convex with small palp, distal margin with 9 teeth having 0, 1, 1, 4, 4, 4, 4, 4, 4 lateral teeth (from outer to inner). Maxilla 2: plates not broadening distally; inner plate setose on inner margin, a row of very fine setae runs parallel with inner margin and distal margin; a stout pilose seta terminates a row of spines which are less curved inwardly than in most talitrid species; outer plate outer margin convex, sparsely pilose, distal margin with a row of inwardly curved spines. Maxilliped: inner plates sub-ovate, narrowing somewhat distally, inner margin with a row of long setae which become larger and pilose distally, this pilose setal row continues parallel to the distal margin but set a little proximally to it until it becomes marginal at the outer distal angle of the plate, 2 spine teeth are set at the distal margin and 1 small spine tooth is medial to these; outer plate has setal comb rows along the distal margin and parallel to the inner margin for about 1/5 of the length of this margin, a group of 4 stouter spines are present on the inner lateral face at 0.5; peduncle segment 1 has 1 spine at outer distal angle, and a group of 3 spines at distal margin, segment 2 has 1 spine at outer distal margin and 2 spines at inner distal angle; the palp curves inward, each segment has a spine at the outer distal angle, and a patch of spines at the inner distal angle, which becomes a setal comb on segments 2 and 3 set on the lobular inner margins; segment 4 distinct and not masked by segment 3.

Gnathopod 1: basos broadening slightly distally, posterior margin spined at 0.43, 0.50, 0.63, 0.74, and 0.86, posterior margin spined at 0.17, 0.50, and 0.73, posterodistal angle with 1 large and 1 small spine; ischium posterior margin convex, with a spine at 0.70, and at distal angle; merus posterior margin convex with 6 spines; carpus anterior margin convex, with 2 spines, anteriordistal angle with 4 stout spines, posterior margin produced distally into a scabrous pellucid lobe, which is protected by about 6 large spines arising from its base, one spine is present on the carpus lateral face; propod broadening distally, posterior margin with stout spines at 0.63 (2), and 0.85 (3), and at posterodistal angle (4), posterior margin produced, especially distally, into a scabrous pellucid lobe protected by stout spines basally and by a row of about 9 spines running axially, palm indistinct, at an angle of about 123°, palmar area convex, flanked by few (about 6) stout spines; dactyl stout, longer than palm, curved towards palm with 1 spine on inner margin and 2 at base of terminal spine.

Gnathopod 2: coxal plate ventral margin convex, with about 6 spines; gill large, multilobed; basos broadens at 0.3, narrows to a shallow waist at 0.8 then broadens distally, anterior margin with spines at 0.35, 0.57, and 0.71, posterior margin naked except for 1 small spine at posterodistal angle; ischium long, recurved anteriorly, spined only at posterodistal angle; merus posterior margin produced distally into a bifid pellucid lobe (partially collapsed in type), 3 spines lie distal of this; carpus anterior margin convex and naked except for 2 small spines at distal angle, posterior margin is produced into a large bifid pellucid lobe, posterior proximal angle has 1 small spine, posterodistal angle has 3 spines on both inner and outer faces; propod anterior margin straight, naked except for about 4-5 spines at distal angle, posterior margin produced into a pellucid lobe, a row of stout spines runs axially along the lateral face, palm short, less than 0.33 propod width, distinct, at an angle of 55°, flanked by a row of about 8 spines; dactyl short, curved towards palm, terminal spine occludes into a recess at end of palm.

Peraeopod 1: coxal plate ventral margin and anterior angle rounded, spined; gill large with 2 elongated lobes; basos slightly expanded distally, slightly curved anteriorly, anterior margin with spines at 0.47, 0.57, 0.65 and 0.73, distal angle with 2 spines, posterior margin with spines at 0.42 and 0.66, distal angle with 2 spines; ischium with 2 spines at posterodistal angle; merus broadening distally, anterior margin slightly convex with spines only at 0.19 and 0.47, distal angle with 2 spines, posterior margin sinuous, spines at 0.17 (2), 0.32 (1), 0.40 (1), 0.56 (2), 0.67 (2), and 0.88 (1), distal angle has 2 large spines; carpus subrectangular, anterior margin naked, distal angle with 2 spines, posterior margin spined at 0.15 (3), 0.37 (1), 0.50 (2), and 0.77 (3), distal angle has 2 stout spines; propod slightly curved posteriorly, anterior margin spined at 0.31 (2), 0.60 (2), and 0.88 (2), distal angle has 3 spines, posterior margin spined at 0.10 (1), 0.22 (2+1), 0.43 (2+1), 0.62 (2+1), and 0.83 (2+1), dactyl conical, nearly straight, with 1 inner spine. Peraeopod 2: coxal plate ventral margin nearly straight but slightly sinuous, with 3 spines; gill large with long distal lobe; basos broadening slightly distally, curved a little anteriorly, anterior margin mainly concave, spined at 0.59 (1), 0.71 (2), and 0.88 (2), posterior margin with a spine at 0.60, and 1 large and 1 small spine at distal angle; ischium rhomboidal, with 2 spines at posterodistal angle; merus broadening distally, anterior margin spined at 0.15 and 0.36, distal angle with 3 spines, posterior margin spined at 0.11, 0.16, 0.35, 0.42, 0.64, and 0.76, distal angle with 2 large spines; carpus subrectangular, anterior margin unspined, nearly straight, distal angle with 2 spines, posterior margin spined at 0.11 (2), 0.27 (2), 0.58 (2), and 0.82 (2), distal angle with 2 large spines; propod slightly longer than carpus, broadest medially, anterior margin spined at 0.25 (2), 0.52 (2), and 0.83 (2), distal angle with 4 spines, posterior margin with larger spines at 0.09 (1), 0.19 (2+1), 0.38 (2+1), 0.62 (2+2), and 0.85 (3+1); dactyl slightly curved posteriorly, with 1 spine on inner margin and 1 small spine on outer margin at base of terminal spine. Peraeopod 3: coxal plate bilobed, anterior margin thickened and spined, ventral angle of anterior lobe sharply curved and spined, ventral margin of posterior lobe more gradually curved and spined; gill smaller than anterior gills, folded but not plicate; basos an inverted pyriform shape, narrowing distally, anterior margin spined at 0.09, 0.20, 0.35, 0.52, 0.62, and 0.73, distal angle with 2 spines, posterior margin spined at 0.18, 0.32, 0.41, 0.53, 0.58, 0.79, and 0.95; ischium with 3 spines at anterior distal angle; merus broadening posterodistally to a spinous lobe, anterior margin nearly straight, spined at 0.15 (2), 0.38 (2), 0.75 (1), and 0.82 (1), distal angle spined, posterior margin spined at 0.38 (1), posterodistal lobe has 1 small and 2 large spines; carpus subparallel, anterior margin spined at 0.19 (1), 0.33 (3), 0.57 (4), 0.79 (1), and 0.86 (2), distal angle spined (1+1), posterior margin spined at 0.67 (1), and at distal angle (1+1), propod slightly longer than carpus, spined at 0.09 (1), 0.17 (2), 0.32 (3), 0.49 (2), 0.68 (3), and 0.87 (3), posterior margin spined at 0.37 (2), 0.61 (2), and 0.88 (2), distal angle with 3 spines; dactyl as for peraeopod 2. Peraeopod 4: coxal plate small, rounded except for proximal margin, ventral margin with 3 spines; gill large, multilobed; basos elongated, subovate, anterior margin spined at 0.23, 0.36, 0.50, 0.58, 0.69, and 0.83, distal angle with 1+1 spines, posterior angle has small spines at 0.24, 0.35, 0.43, 0.67, 0.82, 0.87, and 0.96; ischium anterodistal angle has 2 spines; merus broadening distally, anterior margin spined at 0.08 (1), 0.20 (1+1), 0.41 (1+2), and 0.63 (1+2), distal angle with 2 spines, posterior margin with smaller spines at 0.19, 0.37, and 0.62, distal angle with 2+1 spines, carpus anterior margin spined at 0.10 (2+1), 0.26 (3), 0.43 (3), 0.64 (4), and 0.81 (1), distal angle with 3 large spines, posterior margin spined at 0.37, 0.54, and 0.74, distal angle with 3 large spines, propod longer (15%) than carpus, posterior margin spined at 0.08 (1), 0.16 (2), 0.27 (2+1), 0.39 (2+1), 0.54 (2+1), 0.69 (2+1), 0.81 (2), and 0.89 (2+1), posterior margin spined at 0.16 (2), 0.30 (3), 0.51 (3), 0.71 (3), and 0.92 (3), distal angle with about 5 spines; dactyl with only 1 small spine on inner margin. Peraeopod 5: coxal plate small, ventral margin rounded with few small spines; penal organ square; basos an inverted pyriform shape with both anterior and posterior margins expanded, anterior margin convexly rounded with 6 stout spines, distal angle with 1 stout spine, posterior margin rounded convexly and scalloped, with 10 small spines;

ischium anterodistal angle with 3 spines; merus broadening distally, anterior margin spined at 0.16 (2), 0.34 (3), 0.47 (1), 0.61 (3), and 0.78 (2), distal angle with 3 spines, posterior margin spined at 0.24 and 0.55, distal angle with 3 spines; carpus broadening a little distally, anterior margin spined at 0.14 (2+1), 0.26 (3), 0.40 (3), 0.52 (1), 0.65 (4), 0.78 (2), and 0.89 (1), distal angle has 2 spines, posterior margin spined at 0.32 (1), 0.48 (1), and 0.68 (2), distal angle with 2 spines; propod longer by 35% than carpus, anterior margin spined at 0.12 (2), 0.22 (2), 0.34 (2), 0.46 (2), 0.55 (3), 0.66 (2), 0.77 (2), and 0.93 (3), posterior margin spined at 0.19 (2), 0.30 (2), 0.43 (2), 0.63 (2), 0.80 (2), and 0.93 (2), distal angle with 3 double spines.

Pleopods all present and biramous although narrow and slender; all with 2 coupling spines; first and second equal in length, third smaller (80%); outer margins setose with pilose setae; outer ramus the shorter on each, segmentation on rami poorly developed; rami margins setose with pilose setae.

Epimeral plate 1: subtriangular, acutely angled distally, posterior margin with 2 small spines; Epimeral plate 2: subsquare, anterodistal angle rounded, posterodistal angle acute and slightly produced, posterior margin slightly sinuous with 3 small spines; Epimeral plate 3: subsquare, anterodistal angle rounded, posterior distal angle acute, posterior margin slightly scalloped and with 4 spines.

Uropod 1: slender, peduncle with a row of 4 spines on both dorsal margins, inner ramus with spines at 0.11, 0.25, 0.48, and 0.67, outer ramus with spines at 0.60, and 0.74; a large inter-ramal spur is present; both rami end with 2 larger and 2 smaller terminal spines of which the second largest is scionate. Uropod 2: dorsal margin of peduncle with 2 spines, a small inter-ramal spur is present; both rami spined with scionate spines, rami terminate with 1 larger and 2 smaller spines of which one is scionate. Uropod 3: a simple uniramate tubercle with 2 spines on peduncle and 2 large and 2 small terminal spines on ramus. Telson scarcely bilobed, not cleft, with 3 spines on each lobe arranged so that the 6 spines form a coronal circlet posteriorly.

Cuticular structures (paratype), Figure 392: the epidermal cells of the lateral aspect of abdominal segment 2 form a polygonal outline on the cuticle surface with an average size of 22.7 micrometres by 17.3 micrometres. A thick layer of mucoid secretion is present. Micropores are scattered over the surface, but are indistinct. Mesopores are arranged in a row set back from 2 cuticular polygon boundaries; these pores open vertically. Macropores are present at cell boundaries, at a density of 2116 mm^{-2} on abdominal segment 2, and 3926 mm^{-2} on the uropod 1 peduncle ventral surface.Many macropores are masked by large spherical masses of mucoid secreta.

Female:

Length 16.5 mm, width 3.4 mm, depth 3.4 mm. Antenna 1: length 3.2 mm, as for male but peduncle segment 1 inferior margin with 1 small spine proximally and 3 larger spines distally; peduncle segment 2 with 2 large spines at inferodistal angle, superodistal angle spined; peduncle segment 3 superior margin spined at 0.23, 0.36, and 0.55, inferior margin spined at 0.21 and 0.43, superodistal angle with 3 spines; flagellum of 9 podomere segments. Antenna 2: length 9.7 mm; peduncle segment 3 has 3 spines on inferior margin; peduncle segment 5 superior margin has 4 spines, lateral margin has 5 spines, ventral margin spined at 0.22, 0.30 (2), 0.42, 0.55 (2), 0.67 (2), 0.76, 0.83, and 0.90; flagellum has 29 podomere segments.

Mouthparts: left mandible with 6 inter-dentate pilose setae, admolar setal tuft of pilose setae present, molar 21-striate. Gnathopod 1: basos broadening distally, anterior margin with spines at 0.49, 0.60, 0.69, 0.82, and 0.90, posterior margin with spines at 0.34, 0.45, 0.73, and 0.80; ischium posterior margin convex but naked, distal angle with 4 spines; merus posterior margin convex, spined at 0.27, 0.43, 0.48, 0.64, 0.68, 0.78, and 0.86; carpus broadening posterodistally into a pellucid lobe, with 6 stout spines on the posterior margin, 2 groups of 3 spines and 2 groups of 1 spine on frontal aspect, anterior margin spined at 0.39 (2), and 0.67 (2); propod heavily spined, narrowing distally, anterior margin with spines at 0.35 (2), 0.65 (3), and 0.85 (3), posterior margin with scionate spines at 0.11 (5), 0.35 (5), 0.57 (5), 0.84 (5), and 0.89 (1), a short row of 4 spines runs at an oblique angle to the proximal posterior margin across the lateral face of the segment, palm absent but the dactyl and propod are still at least partially chelate; dactyl longer than distal width of propod, with 1 inner spine and 2 small spines at the base of terminal spine.

Gnathopod 2: broodplate much longer than broad, rounded distally with 10 setae; basos anterior margin spined at 0.21, 0.40, 0.57, and 0.79, posterodistal angle with 3 spines; ischium posterodistal angle with 4 spines; merus posterior margin produced into a pellucid lobe with about 5 spines surrounding base; carpus anterodistal angle with 4 spines, posterior margin produced into a pellucid lobe with 3 spines proximally and 4 larger spines distally; propod long, with naked margins, outer face with a row of stout spines running axially, inner face with a more sparse row running axially to the palmar area, palm small, oblique, recessed into pellucid lobe and masked by a marginal row of about 8 spines, posterior margin of propod produced to a long pellucid lobe which projects well beyond the palm; dactyl short.

Peraeopod 1: broodplate shorter than that of gnathopod 1, rounded distally with 13 setae; basos less curved than in male, anterior margin with spines at 0.56, 0.67, and 0.76, posterior margin with spines at 0.35, 0.51, and 0.75; merus anterodistal angle with 3 spines, posterior margin much less setose than male with spines at 0.26 (2), 0.50 (2), and 0.71 (2), distal angle with 3 spines; carpus anterior margin with 1 spine at 0.54.

Peraeopod 2: broodplate longer than that of peraeopod 1, distal end rounded with 12 spines.

Peraeopod 3: broodplate as long as that of peraeopod 2, distal end rounded with 9 setae; basos proportionately wider than male; merus posterior margin spined at 0.27 and 0.53, lobe at posterodistal angle a little more produced; carpus posterior margin naked; propod anterior margin naked.

Peraeopod 4: broodplate smaller than others, somewhat triangular, narrowing distally, with only 2 much reduced setae;

basos more massive than in male, broader distally; propod anterior margin spined at 0.13 (2), 0.24 (2), 0.38 (3), 0.56 (3), 0.72 (3), and 0.89 (3).

Peraeopod 5: basos proportionately longer than male; merus anterior margin spined at 0.23 (4), 0.46 (4), and 0.66 (4), posterior margin spined at 0.29, 0.43, and 0.65, posterodistal angle produced distally to a lobe bearing 4 spines.

Uropod 1: outer ramus naked; Uropod 2: both rami have 3 spines on dorsal margin; Uropod 3: has only 1 large and 1 small terminal spine on ramus; telson has 4 spines on both lobes.

Remarks

This species is very abundant and very wide spread. Indeed, it may qualify as one of New Zealand's most numerous native terrestrial animals. It has been collected by a large number of collectors, and good examples occur in every collection I have examined. Feminized species are amongst the most successful and abundant terrestrial talitrids. Many earlier workers commented on the highly skew sex ratio in favour of the female. In some cases they were probably examining mixed species collections containing at least one feminized species in addition to the more 'normal' species. Thus, I presume this species was thought to be female *Parorchestia tenuis*, a species with which it is often sympatric. Hurley (1957:172) in his discussion of *Parorchestia tenuis* stated "Specimens from Kapiti Island (and elsewhere) show some minor differences which may be representative of geographical races or sub-species. Apart from differences in the number of telson spines (up to 5) and pleopods (which may have plumose setae or very short bristles along the peduncle margin), the gnathopod of the female may approach the simple condition through a combination of slight lengthening of dactylos and slight reduction of palm." It seems obvious he is referring to T.aotearoa.

Little is known of the ecology of T.aotearoa other than it occurs in very high densities in lowland forest, but not in the pohutukawa strand forest occupied by Kanikania rubroannulata. Above 300 m it occurs with Parorchestia tenuis which partially replaces it at even higher altitudes and in low conductivity soils. It occurs in both podocarp- hardwood and beech forests living in moss and leaf litter. It is also abundant in bush remnants - even those in which the soil has been heavily churned by stock - and in regenerating forests. It is common under bracken fern, Pteridium aquilinum, but is uncommon under grass. It breeds in spring, summer and autumn.

In the Wellington District it is being replaced by the adventive talitrid, Talitroides topitotum, which is now the common urban and suburban landhopper in Auckland City and Wellington City. Collections made by R.K.Dell in Bartons Bush - a heavily damaged, senescent stand of native bush in the Hutt Valley surrounded by suburbs of the Hutt conurbation - show that T.aotearoa was the only landhopper present in 1962 while Talitroides topitotum was not present. In 1982, however, I was unable to find T.aotearoa; the only landhopper present was Talitroides topitotum. The success of

Talitroides topitotum is possibly due, in part, to its aggressive colonising ability in areas disturbed by man. It has a higher reproductive rate than the native landhoppers like *T.aotearoa* and so is better able to withstand the devastation caused by the whitey disease, induced by *Bacillus subtilis*, that it probably brought with it when it invaded New Zealand.

DISCUSSION

Brundin (1966) discussed the relative suitability of different groups of organisms for phylogenetic analysis. He considered that groups which are rich in complex structural systems facilitate phylogenetic analysis. In particular, he considered the holometabolous insect orders to be particularly suitable. His criteria of phylogenetic suitability are worth considering here in relation to landhoppers. These criteria are:

(1) Accessibility and ease of sampling. Modern techniques enable very large samples of landhoppers to be collected.

(2) Cold-resistance. Although talitrids are not as cold resistant as are Brundin's midges, they persist in the subantarctic islands, thus providing very important links with other Gondwana fragments.

(3) Small animals show greater persistence through periods of climatic and geological stress than do larger animals. This certainly applies to landhoppers even though they are many times larger than midges. Even in habitats thoroughly modified by man, they persist in gullies and bush remnants, often at high densities.

(4) No co-evolution with or limitation by food species. Landhoppers feed on plant litter, any litter, providing it is old enough and damp enough, hence co-evolution and exclusion through limitation of plant diversity have not been problems.

(5) Unchangeability of habitats. Cryptozoic habitats persist even though the cryptozoa inhabiting these habitats may have to migrate laterally or vertically (up mountains) in order to survive.

(6) Absolute age. Landhoppers are most likely as old, if not older, than midges, and may even have been contemporaneous with the very earliest land dwellers.

(7) Distribution patterns beyond the influence of man. Some landhopper species have been greatly influenced by man's activities, and this influence is getting greater each year. However, it is still possible to work out most of the details of the distribution of New Zealand landhoppers before the coming of man. But this may not be possible for much longer. is becoming greater with each succeeding decade.

Landhoppers do not have complex life histories as do the holometabolous midges Brundin studied, but we know their plesiomorphic states. Thus, not only is phylogenetic analysis facilitated, but we are also able to discuss the adaptiveness of apomorphic states, something which is usually only possible at grade level or for very old sister groups. Certainly, it is rare to be able to discuss adaptiveness of apomorphic states species by species.

Another advantage possessed by landhoppers is that their evolution seems to have been comparatively slow. They have responded only to the more persistent vicariant events, which facilitates phylogenetic interpretation. There does not seem to be the confusing morass of clines, peripheral populations of dubious systematic status, hybridism or disjunction which afflicts other groups in New Zealand, especially the plants, but this view may be a reflection of the paucity of our knowledge and the crudeness of our techniques. The phylogenetic simplicity displayed may be the deception of ignorance, and not the true pattern of straight forward evolutionary development. Even so, their study would be valuable even if only as a check on the biogeographic and phylogenetic pattern revealed by the study of other, more popular, groups.

General Phylogeny

The general close resemblance of the landhopper to supralittoral species has been remarked on many times and has led to the common belief that they evolved from supralittoral ancestors (Bulycheva, 1957; Hurley, 1959; 1968; Bousfield, 1968; Wildish, 1979; Friend, 1980). Morphological and behavioural similarities (nocturnalism, general decaying matter feeders etc) make this most likely. There is, however, some disagreement concerning details of their origin. Bulycheva (1957) proposed that a *Talitrus* form evolved from a littoral *Hyale*-like ancestor which then gave rise to the other terrestrial genera. Friend (1980) pointed out this scheme involves the loss of chelate gnathopods in the non-chelate Talitrus from the chelate Hyale, then their re-aquisition in the chelate Orchestia form. Such redevelopment of reduced or derived parts, a reversal of evolution, makes for considerable difficulties. Hurley (1959, 1968, 1975) considered that they were possibly polyphyletic in origin, although he concedes in his 1975 paper that the Talitrus group may have had a monophyletic origin in Gondwana. But he still believed that the Orchestia group probably had independent origins from nearby supralittoral species. Friend (1980) considered that landhoppers had a Gondwana origin and explains their absence from Laurasia by their failure to disperse there. He believed that sexually similar species (thought to be the more primitive) could arise from the local supralittoral species in isolated islands of Gondwana regions. He explained the absence of landhoppers from Laurasia by the failure of supralittoral species, which he presumes evolved in Gondwana, to arrive there until late Tertiary times. Thus, in is view, there has not been enough time in the northern hemisphere for local species to arise from the comparatively recently acquired supralittoral fauna. He cited the evidence from Hurley (1959) of an apomorphic species in Jamaica as evidence for an early landhopper fauna in South America, even though Hurley (1975) considered that this species originated from Southern Hemisphere forms and is not endemic.

Friend's hypothesis presents considerable difficulties: how could such an easily and widely dispersed group as the supralittoral talitrids not have reached Laurasia until the late Tertiary, even if they did originate in Gondwana? They appear to have speciated too widely in the Northern Hemisphere for such an explanation to be true. It is more likely, in my opinion, that the supralittoral species are an ancient group common to both northern and southern hemispheres although possibly polyphyletic in origin from different littoral ancestors. If this is so then the explanation for the absence of landhoppers from most of the northern hemisphere must be sought elsewhere. A vicariance hypothesis does provide an explanation assuming that the landhoppers originated in Gondwana and not in Laurasia before Gondwana broke-up and some of its fragments drifted to an extent that they crashed into Laurasia. Their absence from South America proves a difficulty for the vicariance origin hypothesis because this area was once a part of Gondwana and its climate appears perfectly suitable for landhoppers. Hurley (1975) advanced one explanation: that the monophyletic Gondwana group, the _Talitrus_ assemblage, evolved after South America broke off but before the rest of Gondwana broke up. But such a sequence of events does not accord with either the dates or the sequence of the break-up of Gondwana according to Van Andel (1976) who stated that a gap opened south of South America in the Miocene, well after the separation of India in the Cretaceous and of Australia in the late Eocene and early Oligocene. Barker and Burrel (1977) view the opening of the Drake Passage, and the effective isolation of South America from West Antarctica, as having occurred during the

Oligocene. This earlier date is still, however well after the Jurassic-Triassic-Cretaceous break-up of the rest of Gondwana. Thus Hurley's explanation for the distribution of Talitrus does not accord with the known geological facts. If the geological evidence is correct, and if the Talitrus group had a monophyletic origin in Gondwana then they should still be present in South America since they are present in India and Australia, unless some subsequent event has caused extinction in South America. Even if the Talitrus group did not disperse to South America or, if they did and subsequently became extinct, why are there no Orchestia type landhoppers in South America which evolved from the local supralittoral species as Hurley proposes occurred for the Orchestia group in general? Indeed, if his hypothesis is true why are there none of this group in the Laurasian area? An explanation based on restricted distribution due to regional evolution seems to be incomplete.

Probably, landhoppers are ancient animals which evolved from supralittoral forms once the truly terrestrial environments became exploitable, which was in turn determined by the establishment of a terrestrial flora which provided a food source, and protection from excessive ultraviolet light. Even today, New Zealand landhoppers seem to prefer to eat ancient plants like bryophytes and ferns to many of the more modern plants which probably evolved after the talitrids.

Their absence from Laurasia can be explained either by a vicariance hypothesis of their evolution in Gondwana, or by a competitive exclusion hypothesis whereby they were excluded by superior competitors once these had evolved. Possibly Laurasia had landhoppers before insects and modern plants underwent their massive co-evolutionary development, and that they became extinct there because of competition from more recently evolved and better adapted competitors. In support of the competitive extinction hypothesis it may be noted that other groups have become extinct, the ruling reptiles are a classical example, but whereas these groups have usually left traces in the fossil record the boreal landhoppers are unlikely to have done so since the acid nature of the forest soils in which they lived would have dissolved the calcium from their exoskeleton well before fossilisation processes could have preserved their remains. Another similar example is provided by the Onychophora. swapping of faunas which occurred when South America crashed into North America

The view taken here is a composite of both hypotheses; the landhoppers originated in Gondwana, hence their absence from Laurasia, but the/ were subsequently excluded from South America by the composite biota which resulted from the faunal exchange which occurred when South America joined North America in the Permian. Interestingly, the Galapagos Islands still have a landhopper of the plesiomorphic type which may have arisen by local origin from the supralittoral species on the islands themselves, or it may have arrived on the Galapagos by long distance dispersal from South

America before the landhopper fauna became extinct on the mainland.

Considering the detailed ecophysiological path followed by landhoppers in their evolution towards terrestrialism most authorities apparently seem to favour the direct evolution from a supralittoral species. Certainly, strand species may have been originated this way, then these species in their turn, have given rise to coastal and inland species, but such a pathway presents many difficulties of water conservation and ion balance which must be solved all at once. These difficulties are less, however, for versatile estuarine species such as Transorchestia chiliensis. As shown in Part II this species has already reduced the osmotic imbalance between itself and its environment, by lowering its haemolymph osmotic pressure; so it is preadapted to life on land. Possibly then, the least terrestrial species, those of the strand, living in high (electrical) conductivity soils, evolved directly from oceanic supralittoral species, but their adaptations to high conductivity environments may prevent them making deeper incursions into the more terrestrial situations of low conductivity soils. The more terrestrial species had a long and difficult evolutionary path which probably required a massive reduction in blood osmotic pressure and the development of unique ion attainment and conservation mechanisms and special osmotic adaptations for brooding, to say nothing of massive behavioural and ecological adaptations. These huge, if diffuse, ecophysiological barriers would suggest that the terrestrial species did not evolve repeatedly or with considerable ease as implied by many other workers. It should be noted that only a relative few animal groups have succeeded in becoming terrestrial, and most of those that have invaded land are restricted, as are the landhoppers, to the less terrestrial cryptozoic environment. The ecophysiological barriers to the invasion of terrestrial environments are massive. Cryptozoic environments are certainly easier than other terrestrial environments to conquer, but even they present a great challenge for would-be invaders. Possibly, the landhoppers evolved from supralittoral ancestors who had become adapted to environments with a marked fresh water influence, particularly estuarine ones. Such preadaptations would have reduced the intensity of the barriers to successful terrestrial life and made the conquest of land much easier. But because of these barriers there were probably only a limited number of deep incursions into the terrestrial environment.In the New Zealand landhopper fauna we can recognise the groups which all made independent incursions to land: the *Talorchestia*-*Talitrus*-*Talitroides* assemblage, the *Makawe*-*Parorchestia* assemblage (which is equivalent to Hurley's '*Orchestia*') and possibly *Kanikania*. The *Makawe*-*Parorchestia* assemblage left a trail of species adapted in greater or lesser degree to the terrestrial environment. *Kanikania*, and other strand groups, probably had independent origins from oceanic supralittoral ancestors, since adaptation to high conductivity soils may preclude evolution to low conductivity soils. Thus strand groups may be at an evolutionary dead-end. *Talorchestia* has terrestrial species only in New Zealand, and, as considered earlier, the terrestrial members of *Talorchestia* possibly make up the plesiomorphic sister group to the *Talitrus*-*Talitroides* assemblage with which they are allopatric. This explains the point noted by Hurley (1975) that the *Talitrus* group do not have supralittoral forms which resemble them; the explanation advanced here is that they did not derive directly from the supralittoral but instead evolved from an advanced terrestrial form closely resembling *Talorchestia aotearoa* by neoteny.

The Gondwana origin proposed for the 'common track' landhoppers is the same as the vicariance hypothesis proposed by Hooker (1853) to explain the distribution of *Nothofagus*. Like these southern beeches, landhoppers have different regional groupings which could be interpreted as deviations from the common track after the vicariance event, or that multiple vicariance events were involved (for instance, the Gondwana fragments isolated at different times), or that there was already regionalisation within Gondwana before its break-up. A full cladistic analysis using the techniques of Hennig (1966, 1980), and Funk and Brooks (1981) may resolve these different hypotheses. However, such an analysis must await a more complete description of species in other areas.

Isolated oceanic species could have originated vicariously with the loss of land connection between the oceanic islands and the 'main track', or they could have arrived by long-range dispersal mechanisms, or they could have originated directly or indirectly from nearby supralittoral species. With respect to the latter hypothesis both Hurley (1975) and Friend (1980) have considered the possibility that isolated, plesiomorphic species have originated directly from the local (sympatric) supralittoral species. But such an idea is fraught with difficulties since it involves sympatric speciation about which much has been written (White, 1978), but which both Mayr (1979) and Brundin (1981) consider to be a rare mode of speciation if it occurs at all. It is difficult to imagine a well-established supralittoral species breaking into 2 species, one supralittoral and one terrestrial in the face of massive and continuous gene flow on a small island. If a species inhabits both the strand and the supralittoral (especially that with a freshwater influence) then it would tend to adapt to the mode of the conditions at least as far as its osmotic relations are concerned. But as far as its mechanical relations are concerned, then the supralittoral is such a demanding environment that, if the species is to dwell there successfully, then it must adapt to the supralittoral conditions. We would expect to find a species with a predominantly supralittoral morph with an ability to inhabit strand areas. Such species are not rarities, but nor are they terrestrial.

If evolution to land is as difficult as it appears to be how did isolated, oceanic islands get their landhopper fauna? Explanations to account for this include the possibility that terrestrial evolution is not as difficult as proposed here and that isolated landhoppers evolved directly from the supralittoral as proposed by Hurley and Fried. A vicariant origin is also possible, but this is not in accord with the known geological facts of isolated (especially volcanic) islands. Or perhaps the evolution of isolated, primitive, plesiomorphic species may have been from the main track of landhopper evolution on Gondwana, from whence they arrived at their isolated islands by long range dispersal or by the rafting of continental fragments (Nur and Ben-Avraham, 1981). This latter hypothesis presents difficulties according to present-day geological theory (Tedford, 1981). The more primitive strand and coastal species are the most suited to long-range dispersal over oceans because they have a greater tolerance of immersion and salinity. Local origin on isolated islands is possible by an allopatric mechanism. Imagine two isolated islands each with a different species of supralittoral amphipod. In the absence of better adapted terrestrial species, both will evolve to inhabit both the strand and the supralittoral. They will be flexible species inhabiting a habitat gradient from the supralittoral through to terrestrial. If one now disperses into the range of the other, then interspecific competition will cause niche partitioning so that one becomes more terrestrial and one more supralittoral. This could explain the similarity of many isolated species to the supralittoral species in their vicinity because they are closely related phylogenetically. Dispersal of supralittoral species is presumed to be easier than terrestrial species because of their robustness and osmotic adaptations. Under this 'neighbourhood origin' hypothesis, isolated groups are polyphyletic whereas they are monophyletic under the hypothesis of dispersal from centres of origin. It should not be too difficult a task to decide between these hypotheses using the tests devised by Patterson (1982) and others for phylogenetic reconstruction.

Evolution to terrestrialism may be easier on islands with a fringing coral reef even though no sea wrack is present. In such conditions the strand vegetation, particularly coconut palms, grow down to the high tide mark and dead leaves and coconut fibre, rather than algal mats typical of temperate oceanic beaches, litters the ground providing excellent refuge and food for a wide assemblage of organisms including many terrestrial species. The absence of wave action makes it possible for landhoppers living in such environments to break free from the straight-jacket of the need for a robust body form.

Phylogeny within New Zealand

The ecological groups suggested earlier in this work of oceanic supralittoral, estuarine supralittoral, strand, coastal and inland species, appear to relate to the phylogenetic status of the landhopper species found in such habitats. Thus, strand and coastal species tend to be the most primitive, while inland species are the most advanced. This reasoning may appear to be somewhat circular in that we judge the terrestrialness of a species by the conditions in which it lives, but the phylogenetic scheme presented earlier, and by which independent judgements may be made as to the terrestrialness of the species, does not use habitat information in its construction. Indeed, the fact that there is good agreement between phylogenetic position as determined by morphological characters, and habitat occupied, provides another independent check on the general validity of the phylogeny. Thus phylogenies based on apomorphic-plesiomorphic characters, pigmentation, and ecology are all consistent.

Landhoppers probably did evolve in Gondwana. After the proto-New Zealand land mass broke off the rest of Gondwana at about 80 Ma (Molnar et al, 1975; Weissel et al, 1977) it carried with it a primitive coastal or strand landhopper fauna consisting of two main tracks: the *Makawe*-*Parorchestia* assemblage and the *Talorchestia* assemblage. Evidence for this comes from the predominance of primitive forms in southern regions. As the land mass drifted northwards during its long isolation, the New Zealand landhoppers evolved toward an ever more terrestrial form. During this period of drifting, some species would have been isolated on the southern islands as these were formed. While the remainder of the landhopper species on the main land mass continued evolving, as judged by the number of species and their advanced state, those on the southern islands seem to have evolved at a much slower rate. Perhaps this is due to the absence of much inland-type terrestrial environment. It may also be due to the fact that cold climates, though physically harsh, are biotically benign for those species with the requisite adaptations to persist in them, due to limited competition and predation. Furthermore, the subantarctic islands have their climate considerably ameliorated by the surrounding ocean. On these islands selection pressure may have been low allowing the persistence of relatively primitive forms.

On the main New Zealand land mass speciation could have been induced by isolation caused through climate change, island formation, break-up of continuous land masses such as has occurred through submergence in Marlborough, volcanism or other events. Most of these events are too rapid and transient to have affected the evolution of landhoppers since their rate of evolution seems slow compared with other terrestrial groups. For instance, _Parorchestia tenuis_ seems not to have split into regional species by the climatic events of the Pleiocene, Pleistocene and Recent. This may be a false conclusion which will be rectified on closer and more detailed study of this species, but even if _P.tenuis_ is a species group then the component species in the group have not speciated far since they show few differences between regional populations. A more important feature for speciation seems to have been the aridity barrier found in the rain shadow of the Southern Alps. On the eastern side of this barrier there is a group of species, obviously derived from a _P.tenuis_-like ancestor, while on the western side are found species which are also found in North Island.

The Catlins District of Otago seems to be a meeting ground for species from the east coast and the west coast of South Island as well as Stewart Island. The number of species is far greater here than in most other places in New Zealand. This is not to say that it is a centre of evolution; rather it seems to be that many species have overlapping ranges in this heavily-forested moist coastal region of varied topography.

Northland, however, does seem to be a centre of evolution. This region is a series of linked false islands and seamounts each of which would once have been isolated, perhaps repeatedly. Its mild, damp climate and dynamic geology with a long history of island-forming processes and volcanism, has made it an area where landhoppers have speciated extensively. Solem and Climo (1981) and Climo (pers. comm.) have found that land snails have speciated extensively in Northland.

Much of the North Island has a depauperate landhopper fauna consisting of only one or two species: usually *Talorchestia aotearoa* coastally and *Parorchestia tenuis* inland. There are possibly a few relict species, like *Tara taranaki*, which have yet to be discovered on isolated mountains or hill regions, or even in isolated patches of forest. The cause of the depauperisation over much of the North Island could have been ash showers and the massive lava flows from the Taupo volcanic eruptions. However, the region south of the area affected by recent volcanism is still depauperate, with the same species occurring there as in the volcanic plateau. In the Aorangi Mountains, for instance, the same two species, *T.aotearoa* and *P.tenuis*, occur as do on the Volcanic Plateau. Cook Strait is a very recent feature dating from the late Pliocene (Stevens, 1980), and is no barrier to these two species which are also abundant in Marlborough and its islands, Nelson, and Westland-Canterbury on both sides of the main divide. Mountain chains are not barriers to these two, wide-spread species since both can occur well above the bush line, and so can disperse from one side of the chain to another via mountain passes. On the other hand, inter-montane basins can be very arid, and are likely to be significant dispersal barriers isolating populations on the forested upper slopes of isolated mountain chains on the Canterbury side of the Southern Alps from the forested foothills far nearer the coast. The forests of the main divide and those of the coastal foothill are separated by an extensive area of arid mountains and inter-montain basins. Few suitable areas for landhoppers occur here. These areas are poorly known biologically but may contain new species.

At the Kaikoura mountain ranges there is a well-defined transition from the northern species to a cluster of species which occur only on the eastern side of the South Island. To the south these eastern species have no common terminating boundary, thus M.otamatuakeke stops at Dunedin being replaced south of there by P.tenuis while M.hurleyi straggles to Southland coastal sites. Thus the South Otago coast marks a region of great overlap between northern P.tenuis, eastern M.hurleyi and southern Talorchestia patersoni elements. Stewart Island is the centre of a southern element which includes the primitive T.patersoni and K.motuensis and the advanced P.tenuis and P.longicornis. Endemism is very high on the subantarctic islands and the species are, in general, primitive.

Using the technique developed by Platnick and Nelson (1978) area and taxa cladograms are given for Talorchestia in Figure 393. This indicates an early vicariance event (1), which can be identified with the Mesozoic break-up of Gondwana. Then a second vicariance event occurred (2), in which the southern forms leading to T.patersoni (A) were separated from the northern forms, north of the Kaikoura Orogeny which occurred in the late Miocene. Pliocene times (Gage, 1969). Finally a third vicariance event occurred to the southern forms with the isolation of the Snares Islands. This event did not affect the northern forms. The sister group line (D) in other areas of Gondwana after the separation of New Zealand, evolved through neoteny to the _Talitrus-Talitroides_ assemblage which explains their simple first gnathopods and mitten-shaped second gnathopods in both sexes. Juvenilisation of an _Orchestia_ form would not lead to the simple condition of the first gnathopods because these adopt other useful functions once carrying copulation is abandoned. The _Talorchestia-Talitrus_ assemblage seem to show a much more marked "all-or-none" response to reductionist trends than do the _Orchestia_ assemblage, which implies a far less subtle control over the developmental rate genes. _T.patersoni_ has lost all its pleopods which appears to be going too far! The _Talorchestia-Talitrus_ assemblage therefore, shows a canalised evolutionary tendency or 'unique inside parallelism' (Brundin, 1981) different to that of the _Orchestia_ complex.

The agreement of the two cladograms is, according to Nelson and Platnick (1981), evidence for the vicariance model, a conclusion which is further strengthened by the concurrence of the geological events which could have been the vicariance events causing the phylogenetic patterns seen in _Talorchestia_.

Interpreting the phylogeny of the '_Orchestia_' assemblage according to the vicariance model is much more complicated because there are very many more forms, and because effective isolation can occur within a geographical area due to ecological factors such as

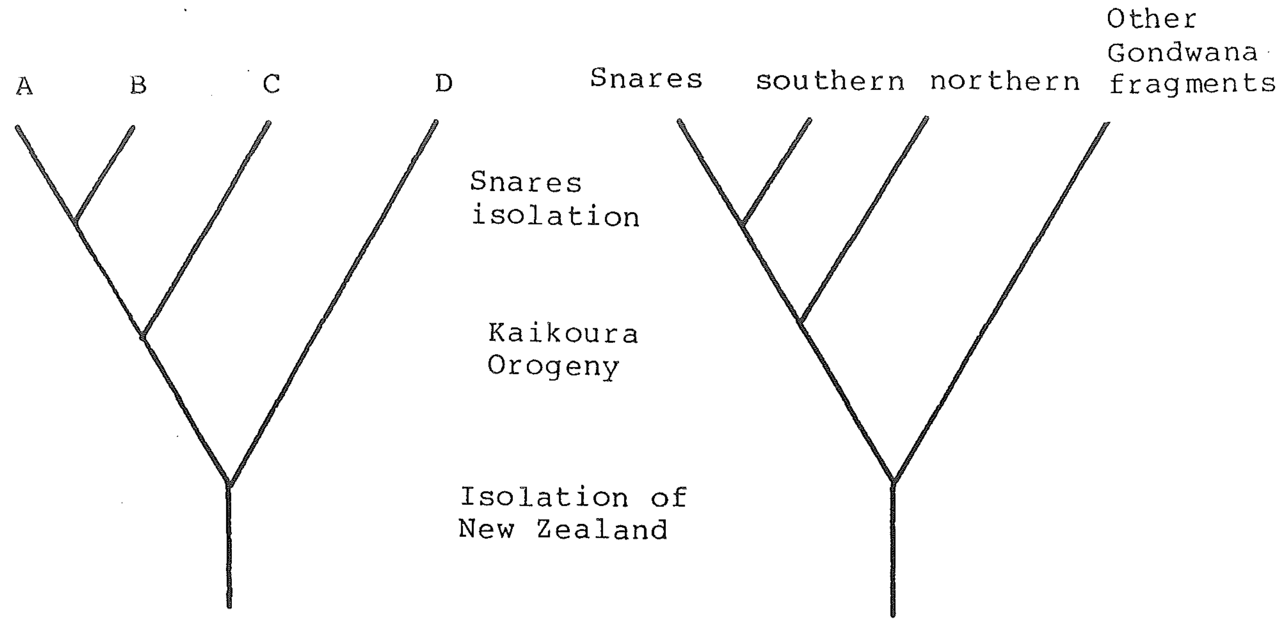


Figure 393. Taxa and area cladograms for Talorchestia. A = T.patersoni snaresi, B = T.patersoni primus, C = T.aotearoa, D = Talitrus-Talitroides group.

the conductivity of the soil. However, the phylogenies in Figures 394 and 395 imply that neither a vicariant nor a dispersalist model is solely appropriate. Instead, there seems to have occurred a sequential anagenic (White, 1978) evolution into, or spanning, new more terrestrial environments. This was not a dispersalist event since the new, organisms had to become progressively more adapted to the barrier, which is made up of more terrestrial conditions, not pass over it. In fact the barrier became part of their range.

This kind of phylogeny is distinct enough to be given a new name - gressive phylogeny, from the Latin meaning step or course. Gressive evolution is a temporal sequence of niche partitioning

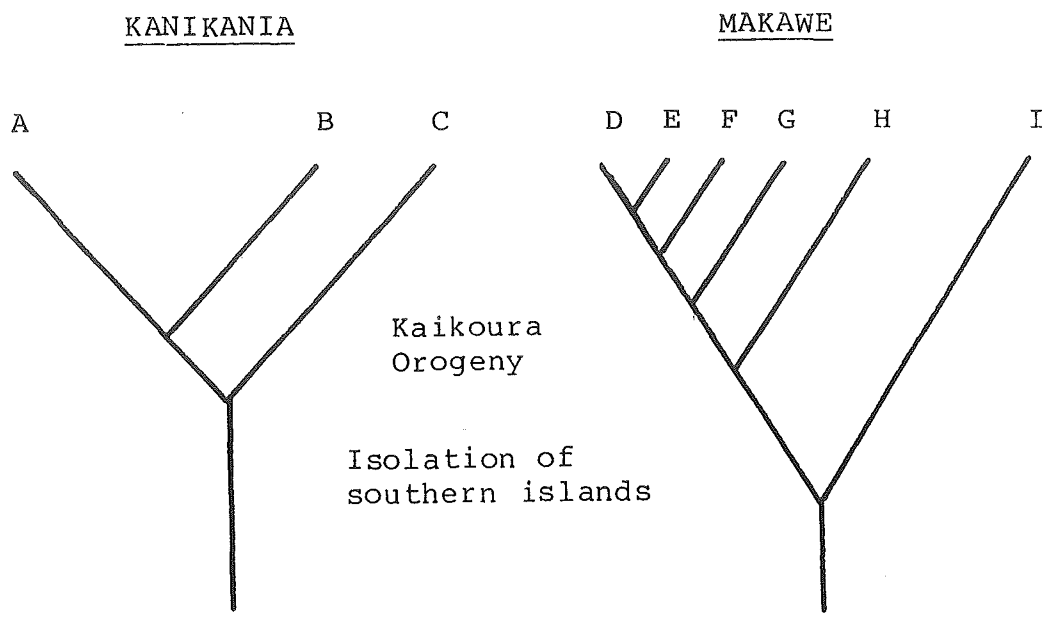


Figure 394. Cladograms for the landhopper genera Kanikania and Makawe. A = K.rubroannulata (North I.), B = K.motuensis (Stewart I.), C = K.improvisa (Snares I.), D = M.hurleyi (east South I., Chatham Is.), E = M.parva (Auckland I.), F = M.insularis (Auckland and Campbell Is.), G = M.waihekensis (Waiheke I.), H = M.maynei) (Stewart I.), I = M.otamatuakeke (foothills, east South I.).

which occurs sympatrically and which results in the development of apomorphic character states without the occurrence of plesiomorphic sister groups in species occupying part of an extensive gradient in environmental conditions. This mode of speciation begins with a species occupying one end of a gradient of environmental conditions, for example the supralittoral end of the supralittoral-terrestrial gradient. The species may, in time, make a partial incursion to slightly more terrestrial conditions. Probably, it would still be occupying its old range, and gene flow would be continuous throughout the population. The new genes of genotypes selected for the new conditions would make the species less well adapted for the original conditions which it still occupies. If an invasion, through dispersal, of a less terrestrial species now takes place, the invading species being better adapted for the less terrestrial conditions, then the original species will tend to be excluded or displaced from its original range and forced, by competition, to occupy its new range (the previous barrier) exclusively. It has undergone a forced evolutionary dispersion and the result is that the original species occupies the more terrestrial conditions inland while its original range is now occupied by a less terrestrial species which originated outside the area. There will be considerable overlap between the two species, as is common in the ranges of landhoppers, because the barriers are quantitative entities, gaining intensity over a distance; they are not usually sudden, abrupt changes in conditions.

Gressive evolution would be allopatric initially, but in contrast with 'normal' allopatric speciation, the whole population is involved not merely a small peripheral fragment of it. Furthermore, the changes in conditions are gradual, not abrupt as is conceived by many authorities for normal allopatric speciation. Gressive evolution is evolution without speciation in which the evolving population is freed from many of the dangers in allopatric speciation outlined by Mayr (1963). There are few risks because the population is large, and the changes are gradual. Gressive evolution should not be regarded as being progressive since it is probably the weaker competitor species which is forced to occupy the more terrestrial habitat.

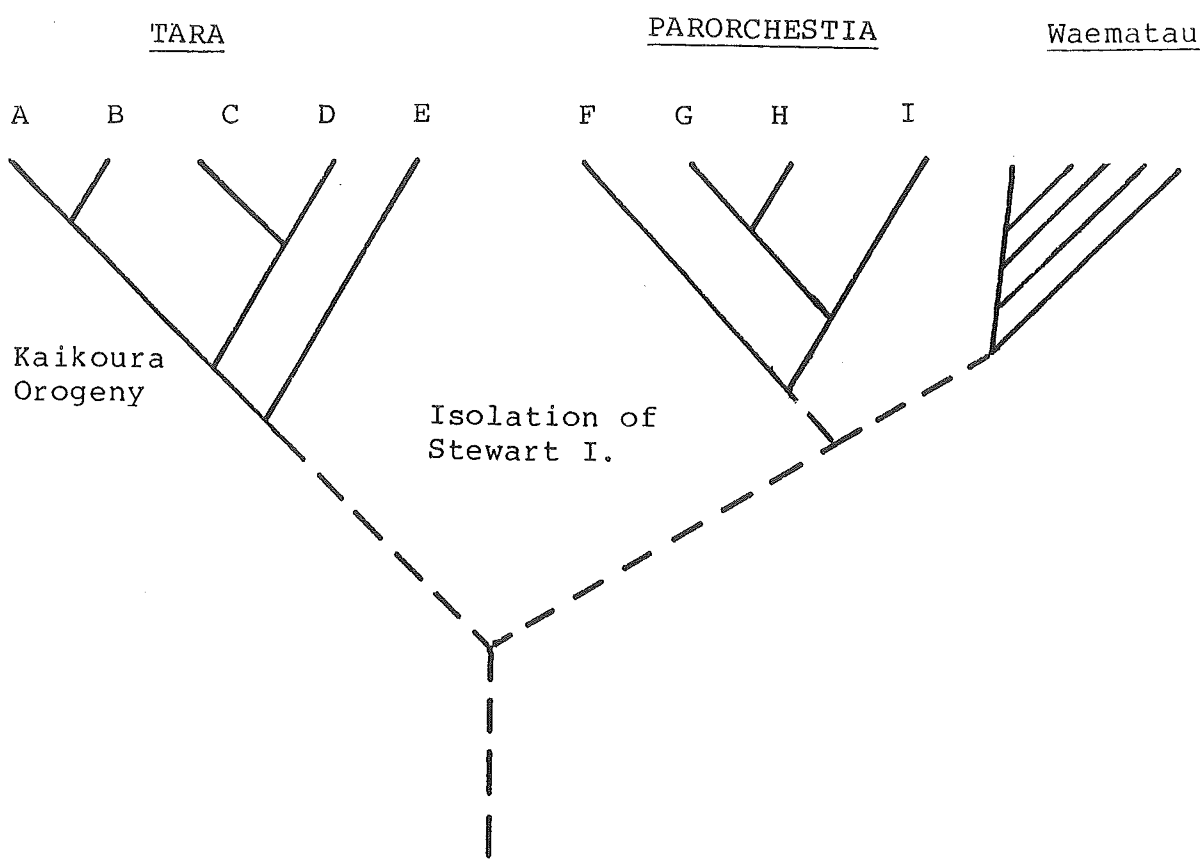


FIGURE 395. Cladograms for Tara, Parorchestia and Waematau. A = T.hauturu, B = T.sylvicola, C = T.taranaki, D = T.sinbadensis, E = T.simularis, F = P.tenuis, G = P.lesliensis, H = P.ihurawao, I = P.longicornis. The Waematau complex is shown only diagrammatically.

Of great phylogenetic interest is the fact that gressive evolution would result in a species adopting apomorphic character states without the development of plesiomorphic sister groups. No dichotomy of species is involved, which makes it a fundamental exception to traditional Hennigian cladistics. The existence of a conceivable exception to Hennigian schemata (cladograms) means that the phylogenies presented in this work should be regarded as tentative.

Following possible gressive development of the main stem of the *Parorchestia* assemblage, *Waematau* may have separated from *Parorchestia* in Northland by a vicariance event, which may have been the isolation of Northland by marine transgression of the Auckland isthmus or widespread and prolonged eruption of the Auckland volcanic field. Subsequently, *Waematau* speciated regionally by a series of binary or reticulate vicariance events which may be related to the great geological activity in the area. *Parorchestia* had earlier responded to the Kaikoura Orogeny by forming the *tenuis* and the *ihurawao* sister groups. *P.tenuis* subsequently speciated into *longicornis* and *tenuis* proper when Stewart Island became isolated. *P.tenuis* has dispersed widely subsequent to speciation into Northland, coastal Otago, and Stewart Island. If *P.tenuis* is present on the Snares Islands then it probably arrived by dispersal mechanisms rather than being present vicariously.

The two less terrestrial genera, Kanikania and Makawe, contain the majority of the southern forms. Their phylogenies are illustrated in Figure 394. Again there is considerable evidence that vicariance is an appropriate model for these groups, but there has been subsequent dispersion especially into areas occupied by more terrestrial species which have thus been forced to undergo gressive evolution into new, more terrestrial areas.

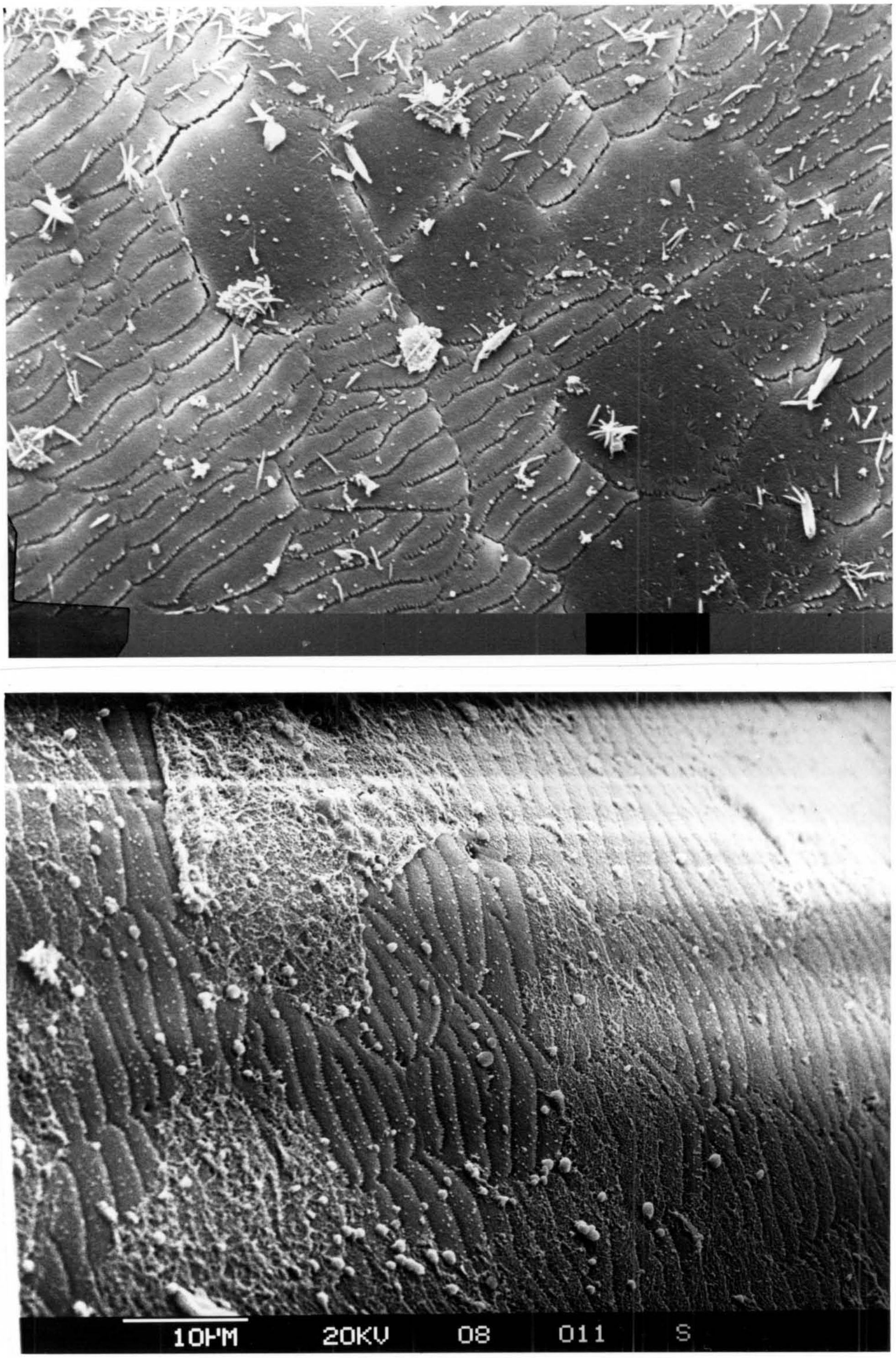
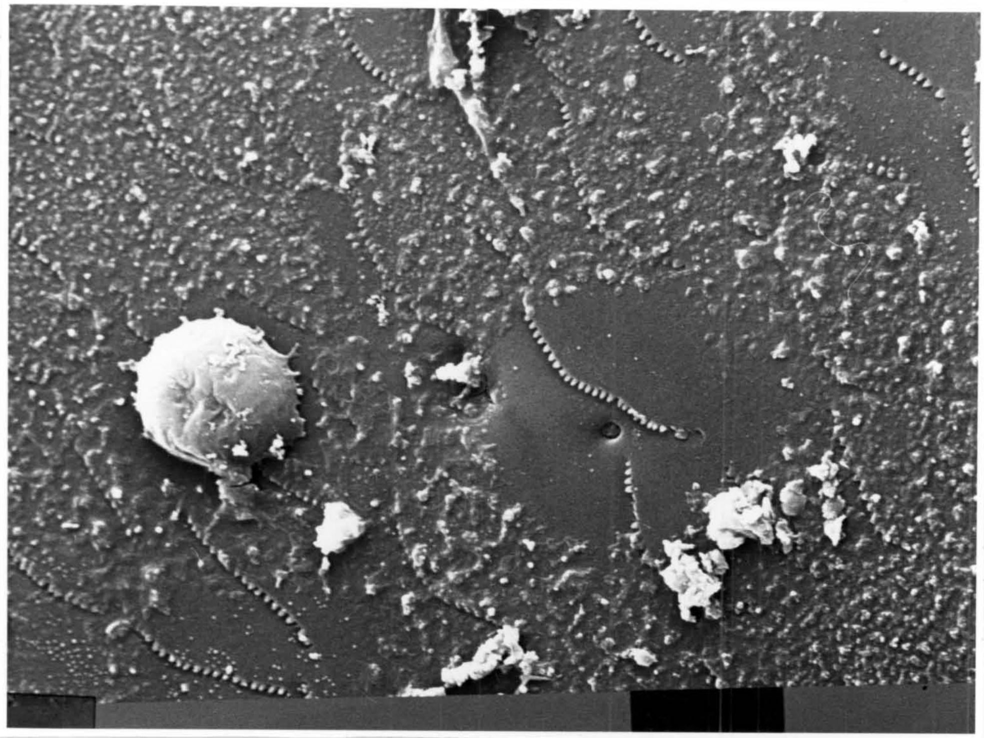


FIGURE 396. Cuticular structures of *Parorchestia ihurawao* uropod 1. The upper micrograph shows the cuticular polygon boundaries and the mesopore 'arcs' are arranged in multiple parallel lines in each polygon. Each mesopore is overhung by a 'veranda'. The lower micrograph shows macropores scattered over the surface as well as the multiple mesopore arc arrangement.



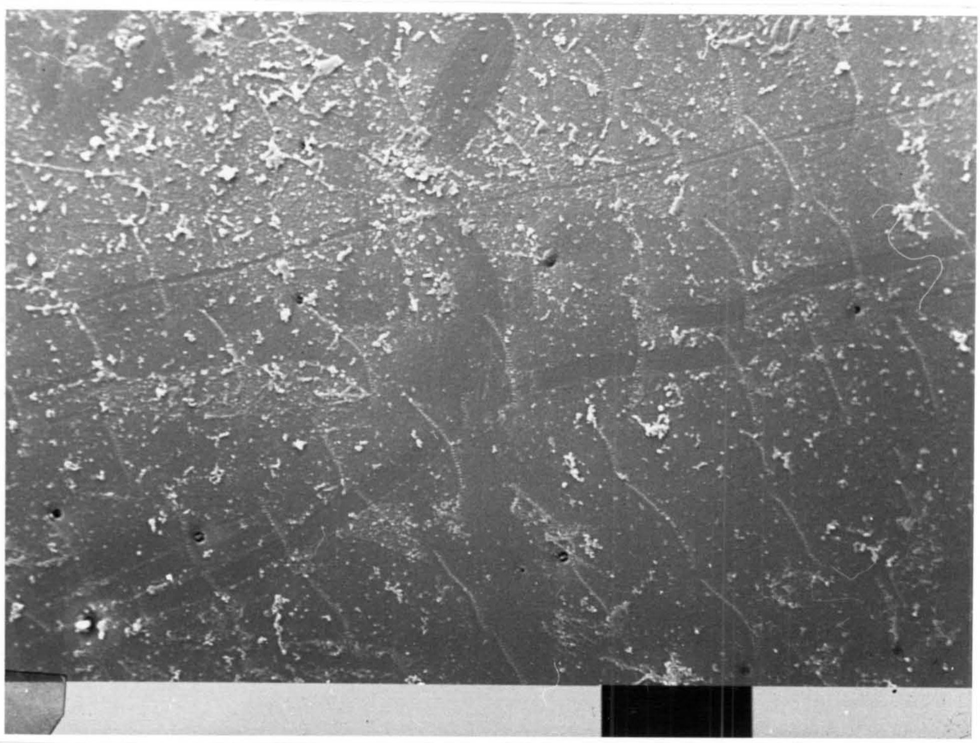


FIGURE 397. Cuticular structures of Talitroides topitotum. The upper micrograph shows the midlateral surface of abdominal segment 2. Macropores are present, and mesopores are arranged into definite arcs protected by 'verandas'. Much mucoid material is present. The scale bar indicates 9 micrometres. The lower micrograph is of the ventral surface of uropod 1 and shows a high density of macropores. The scale bar indicates 18 micrometres.

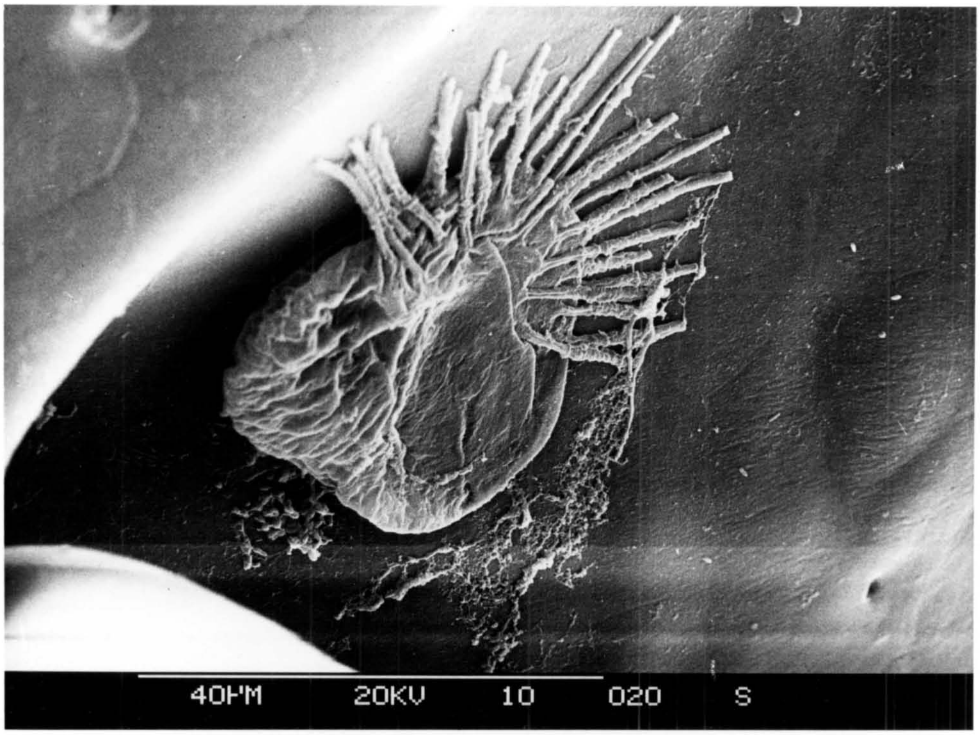


FIGURE 398. An ectoparasite in the depression at the base of a dorsal spine on the peduncle of uropod 1 of Waematau unuwhao.

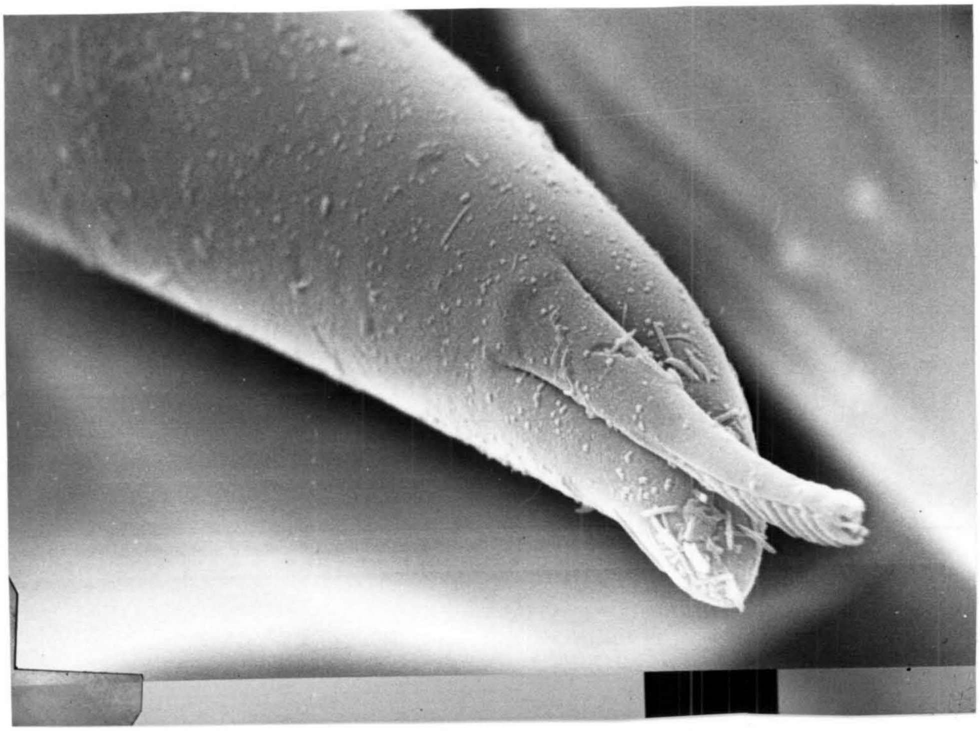


FIGURE 399. Scionate (bifid) spines on Talorchestia aotearoa uropod 1 distal (terminal spines). The scale bar represents 7.5 micrometres.

KEY TO THE LANDHOPPERS OF NEW ZEALAND

1a. Gnathopod 1 simple in both sexes, body pigmentation striped.
..................................*Talitroides topitotum* (adventive)

1b. Gnathopod 1 chelate in one or both sexes, body pigmentation striped or reticulated....................................... 2

2a. Gnathopod 1 simple in female, subchelate in male........... 3

2b. Gnathopod 1 chelate in both sexes..........................4

3a. Gnathopod 2 mitten-shaped in both sexes.....................
.... *Talorchestia aotearoa* (North I., west coast South I.)

3b. Gnathopod 2 propod expanded in male .... *Talorchestia patersoni* (east coast South I., Stewart I., Snares I.)

4a. Palm on male gnathopod 1 oblique, strongly developed; strand species found in high conductivity soils especially on off-shore islands; body pigmentation may be strongly hooped or striped, genus *Kanikania*............................... 5

4b. Palm on male gnathopod 1 transverse, body pattern hooped, spotted or reticulate..................................... 7

5a. Uropod 1 outer ramus naked ....
.... <u>Kanikania</u> <u>motuensis</u> (Stewart I.)
5b. Uropod 1 outer ramus spined 6

6a. Large-bodied species; pleopods all present..................
.... <u>Kanikania</u> <u>improvisa</u> (Subantarctic Is.)
6b. Small species; pleopod 2 and 3 reduced to a vestigial stump
.... <u>Kanikania</u> <u>rubroannulata</u>
(North I. including off-shore islands)

7a. Pleopod peduncles setose; mainly coastal species......... 8
7b. Pleopod peduncles naked or finely pilose; mainly inland
species 13

8a. Uropod 1 outer ramus with dorsal marginal spines; gnathopod 2
mitten-shaped in both sexes.............................. 9
8b. Uropod 1 outer ramus naked dorsally although terminal spines
still present, male gnathopod 2 chelate.................. 10

9a. Outer ramus of uropod 1 with more than 3 spines on dorsal margin; pleopod 3 outer ramus margin with some or many marginal spines; gnathopod 1 propod expanded in male; antenna 1 reaches end of peduncle segment 4 of antenna 2 or just beyond; epimeral plate posterior margin nearly straight..................Makawe hurleyi (east coast South I.)

9b. Outer ramus of uropod 1 with only 1, 2 or 3 spines on dorsal margin; pleopod 3 very reduced; gnathopod 1 relatively slender in both sexes; antenna 1 does not reach peduncle segment 4 of antenna 2; epimeral plate 3 posterior margin emarginate..................Makawe waihekensis (Waiheke I.)

10a. Uropod 2 outer ramus naked, or only very weakly spined (less than 2 spines) dorsally in very old specimens.......... 11

10b. Uropod 2 outer ramus strongly spined with many more than 2 spines.........................Makawe parva (Subantarctic I.)

11a. Uropod 2 inner ramus with 2 rows of dorsal spines...... 12

11b. Uropod 2 inner ramus with a single row of dorsal spines .... Makawe insularis (Subantarctic Is.)

12a. Male gnathopod 2 propod mitten-shaped, telson with terminal spines only......................*Makawe otamatuakeke* (Oamaru)

12b. Male gnathopod 2 propod greatly expanded; telson with marginal spines as well as terminal spines.................. .... *Makawe maynei* (Subantarctic Is.)

13a. Uropod 1 outer ramus spined dorsally; inter-ramal spur on uropod 1 absent. Genus *Tara*............................... 14

13b. Uropod 1 outer ramus naked dorsally, although terminal spines still present; inter-ramal spine may or may not be present... 17

14a. Male gnathopod 2 propod produced 15

14b. Male gnathopod 2 propod mitten-shaped like female........ 16

15a. Uropod 1 heavily spined (Fig 196)......................... ....*Tara taranaki* (Mt. Egmont)

15b. Uropod 1 lightly spined (Fig 168)......................... ....*Tara sylvicola* (Northland)

16a. Antenna 1 extends to beyond peduncle segment 4 of antenna 2; uropod 1 and 2 heavily spined dorsally.. <u>Tara</u> <u>hauturu</u> (Northland)

16b. Antenna 1 extends just to end of peduncle segment 4 of antenna 2; uropod 1 and 2 lightly spined dorsally.. <u>Tara</u> <u>simularis</u> (Subantarctic Is.)

17a. Uropod 2 outer ramus spined dorsally. Genus <u>Waematau</u>..... 18

17b. Uropod 2 outer ramus naked dorsally although terminal spines still present. Genus <u>Parorchestia</u>....................... 22

18a. Inter-ramal spur present on uropod 1..................... 19

18b. Inter-ramal spur absent on uropod 1; pleopod 2 and 3 reduced to vestigial stumps (Figs 293,294))... <u>Waematau</u> <u>unuwhao</u> (Northland)

19a. Male gnathopod 2 mitten-shaped like female.............. 20

19b. Male gnathopod 2 propod expanded, strongly chelate, not like female.. 21

20a. Pleopod 3 a vestigial triangular stump; inter-ramal spur on uropod 1 extends 0.5 way along rami; gnathopod 1 finger (dactyl) extends well beyond margin of strong propod..........................._Waematau reinga_ (Northland)

20b. Pleopod 3 a vestigial cylinder; inter-ramal spur on uropod 1 extends 0.33 way along rami; gnathopod 1 finger does not reach beyond margin of propod................................ .... _Waematau espiratus_ (Northland)

21a. Telson with 2 spines per lobe; pleopods almost naked .... _Waematau kaitaia_ (Northland)

21b. Telson with more than 2 spines per lobe; pleopods relatively densely setose................. _Waematau triregis_ (Northland)

22a. Male gnathopod 2 propod not produced, mitten-shaped like female 23

22b. Male gnathopod 2 propod produced, not like female .... _Parorchestia tenuis_ (North & South & Stewart Is., ?Snares I.)

23a. Antenna 2 has fewer than 30 podomere segments in adult; pleopods narrow or reduced................................ 24

23b. Antenna 2 with more than 30 podomeres in adult; pleopods broad...................._Parorchestia longicornis_ (Stewart I.)

24a. Body strongly reticulated; pleopod 3 vestigial..............
...*Parorchestia lesliensis* (South I., and southern North I.)

24b. Body dotted; pleopod 3 biramous............................
.... *Parorchestia ihurawao* (North Otago)

REFERENCES

ALFONSO,O., 1977. Contribution to the study of Amphipoda from the Azores. Description of a new species. Publicacoes do Instituto de zoologia 'Dr.Augusto Nobre', Faculdade de ciencia, Universidade do Porto, 135:1-32.

ATKINSON,I.A.E.& B.D.BELL, 1973. The offshore and outlying islands. In: The Natural History of New Zealand. G.R.Williams (ed.). A.H.& A.W.Reed, Wellington, New Zealand, pp 372-392.

BARKER,P.F.& J.BURREL, 1977. The opening of the Drake Passage. Marine Geology, 25(1-3):15-34.

BARNARD,J.Laurens & Charline M.BARNARD, 1982. Revision of Foxiphalus and Eobrolgus (Crustacea: Amphipoda: Phoxocephalidae) from American Oceans. Smithsonian Contributions to Zoology, No.372.

BARNARD,K.H., 1916. Contributions to the Crustacean fauna of South Africa. 5.The Amphipoda. Annals of the South African Museum 15(3), No.3:105-302.

BARNARD,K.H., 1940. Contributions to the Crustacean fauna of South Africa.XII. Annals of the South African Museum, 32(5),No.18:381-543.

BATE,C.Spence, 1862. Catalogue of the specimens of amphipodous Crustacea in the collection of the British Museum. British Museum (Natural History), London, 399 pp.

BIERBAUM,C.K., 1980. Occurrence of the tramp terrestrial amphipods Talitroides alluaudi and Talitroides topitotum Amphipoda

Talitridae in South Carolina U.S.A. Brimleyana, 3:107-112.

BOUSFIELD,E.L., 1964. Insects of Campbell Island. Talitrid amphipod crustaceans. Pacific Insects Monograph, 7:45-57.

BOUSFIELD,E.L., 1982. The amphipod superfamily Talitroidea in the Northeastern Pacific Region. I. Family Talitridae: Systematics and distributional ecology. National Museums of Canada, Ottawa, Publications in Biological Oceanography, No.11, 73pp.

BOUSFIELD,E.L.& F.G.HOWARTH, 1976. The cavernicolous fauna of Hawaiian lava tubes. Part 8. Terrestrial Amphipoda Talitridae including a new genus and species with a note on its biology. Pacific Insects, 17(1):144-154.

BOWMAN,T.E., 1977. Orchestia vaggala, a new land hopper from the Galapagos Islands (Crustacea: Amphipoda: Talitridae). Proceedings of the Biological Society of Washington, 90(3):658-668.

BROTHERS,R.N.& M.DELALOYE, 1982. Obducted ophiolites of North Island, New Zealand: origin, age, emplacement and tectonic implications for Tertiary and Quaternary volcanicity. New Zealand Journal of Geology and Geophysics, 25:257-274.

BRUNDIN,Lars, 1966. Transantarctic relationships and their significance as evidenced by Chironomid Midges. Kungl.Svenska vetenskapsakademiens handlinger Fjarde 4 ser.Bd.11.nr.1, Almqvist & Wiksell, Stockholm, 472pp.

BRUNDIN,Lars Z., 1981. Croizat's Panbiogeography versus Phylogenetic Biogeography. In Vicariance Biogeography, A Critique. Gareth Nelson & Donn E.Rosen (eds.), Columbia

University Press, New York. pp 94-138.

BULYCHEVA,A.I., 1957. Morskie biokhi moreii SSSR i sopredel'nykh vod (Amphipoda - Talitroidea). O pred.Faune SSSR, 65:185pp.

CHARIG,A.J., 1982. Systematics in biology: a fundamental comparison of some major schools of thought. In Problems of Phylogenetic Reconstruction, pp 363-340. K.A.Joysey & A.E.Friday (eds.), The Systematics Association Special Volume No.21. Academic Press, London & New York.

CHARNIAUX-LEGRAND,Helene, 1952. Le cycle d'intermue des Amphipodes et ses particularite chez les formes terrestres (Talitridae). Archives de zoologie experimentale et generale. Notes et Revue, 88(4): 178-204.

CHILTON,C., 1909. The Crustacea of the Subantarctic Island of New Zealand, Vol.2. Philosophical Institute of Canterbury, Christchurch, pp 601-645.

CHILTON,C., 1911. The Crustacea of the Kermadec Islands. Transactions of the New Zealand Institute, 43:544-573.

CHILTON,C., 1916. A new species of Orchestia. Transactions of the New Zealand Institute, 48:354-359.

CHILTON,C., 1920. A small collection of Amphipoda from Juan Fernandez. In Natural History of Juan Fernandez and Easter Island. Carl Skottsberg (ed.), 3:81-92.

CHILTON,C., 1921. Amphipoda, Fauna of Chilka Lake. Memoirs of the Indian Museum, 5(8):519-558.

CHILTON,C., 1927. Zoology of Canterbury, General Introduction. In Natural History of Canterbury, pp 166-181.

COCHRANE,G.Ross, 1973. The general environment and biogeography.

In The Natural History of New Zealand. Gordon R.Williams (ed.), A.H.& A.W.Reed, Wellington, pp 1-27.

COCKAYNE,L., 1908. Report on a botanical survey of the Waipoua Kauri Forest. N.Z.Department of Lands, Government Printer, Wellington, 44pp.

CROIZAT,L., G.NELSON & D.E.ROSEN, 1974. Centers of origin and related concepts. Systematic Zoology, 23(2):265-287.

CUADRAS,J., 1982. Microtrichs of Amphipod Crustacea. Morphology and distribution. Marine Behaviour and Physiology, 8:333-343.

DAHL,E., 1973. Presumed chemosensory hairs in talitrid amphipods (Crustacea). Entomologica Scandinavica, 4(3):171-180.

DANA,J.D., 1852. Conspectus Crustaceorum quae in Orbis Terrarum circumnavigatione, Carola Wilkes e Classe Reipublicae Foederatae Duce, lexit et descripsit Jacobus D.Dana. Pars III. Proceedings of the American Academy of Arts and Sciences, 2:201-220.

DANA,J.D., 1853 & 1855. Crustacea. U.S.Exploring Expedition, 13(2):690-1018.

DE BEER,G.R., 1958. Embryos and Ancestors. 3rd ed., Oxford University Press, London, 179pp.

DE CASTRO,A.L.& V.F.G.C.PEREIRA, 1978. Terrestrial Amphipoda of the genus Talitrus introduced into Brasil, Amphipoda Talitridae. Atas da Sociedade de biologia do Rio de Janeiro, 19(12):47-50.

DELLA VALLE,A., 1893. Gammarini del Golfo di Napoli. Fauna und Flora des Golfes von Neapel, 20:948pp.

DINGERKUS, Guido, 1982. Preliminary observations on acidification of alcohol in museum specimen jars. Curation Newsletter, 5:1-3.

DUNCAN,K.W., 1969. The ecology of two species of terrestrial Amphipoda (Crustacea: Family Talitridae) living in waste grassland. Pedobiologia, 9:323-341.

DUNCAN,K.W., 1981. The effect on _Orchestia hurleyi_ (Amphipoda: Talitridae) of a whitey disease caused by _Bacillus subtilis_. New Zealand Journal of Zoology, 8:517-528.

FLEMINGER,A., 1973. Patterns, number, variability and taxonomic significance of integumental organs (sensilla and glandula pores) in the genus _Eucalanus_ (Copepoda, Calanoidea). Fishery Bulletin, 71:965-1010.

FRIEND,J.A., 1979. Two new terrestrial species of _Talitrus_ (Amphipoda: Talitridae) from Tasmania. Papers and Proceedings of the Royal Society of Tasmania, 113:85-98.

FRIEND,J.A., 1980. The taxonomy, zoogeography and aspects of the ecology of the terrestrial amphipods (Amphipoda: Talitridae) of Tasmania. Ph.D.Thesis, University of Tasmania, Hobart.

FRIEND,J.A., 1982. New terrestrial amphipods (Amphipoda: Talitridae) from Australian Forests. Australian Journal of Zoology, 30:461-491.

GAGE,M., 1969, Rocks and landscape. _In_ The Natural History of Canterbury. G.A.Knox (ed.), A.H.& A.W.Reed, Wellington, pp 1-43.

GATENBY,J.B.& H.W.BEAMS (eds.), 1950. The Microtomist's Vade-mecum. J.& A.Churchill Ltd., London, 753pp.

GRIMMETT,R.E.R, 1925. Forest floor covering and its life.

Transactions of the New Zealand Institute, 56:423.

HENNIG,W., 1966. Phylogenetic Systematics. D.Dwight Davis & Ranier Zangerl (tr.), University of Illinois Press, Urbana, 263pp.

HURLEY,D.I., 1957. Terrestrial and littoral amphipods of the Genus Orchestia, Family Talitridae. Transactions of the Royal Society of New Zealand, 85(1):149-199.

HURLEY,D.E., 1959, Notes on the ecology and environmental adaptations of the terrestrial Amphipoda. Pacific Science, 13(2):107-129.

HURLEY,D.E., 1968. Transition from water to land in amphipod crustaceans. American Zoologist, 8(3):327-353.

HURLEY,D.E., 1975. A possible subdivision of the terrestrial genus Talitrus (Crustacea Amphipoda: Family Talitridae). New Zealand Oceanographic Institute Records, 2:157-170.

KESSEL,R.G.& C.Y.SHIH, 1976. Scanning Electron Microscopy in Biology. Springer Verlag, New York. 345pp.

LEACH,W.E., 1813-14. Article: Crustaceology and Appendix. Edinburgh Encyclopedia, 7:383-437.

LILLIE,A.R., 1980. Strata and Structure in New Zealand. Tohunga, Auckland. 441pp.

MACARTHUR,R.H.& E.O.WILSON, 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, 203pp.

McLAUGHLIN,P.A., 1980. Comparative Morphology of Recent Crustacea. W.H.Freeman & Co., San Francisco. 177pp.

MAUCHLINE,J., 1977. The integumental sensilla and glands of pelagic Crustacea. Journal of the Marine Biological

Association of the United Kingdom, 57:973-994.

MAUCHLINE,J.& A.R.S.BALLANTYNE, 1975. The integumental organs of amphipods. Journal of the Marine Biological Association of the United Kingdom, 55:345-355.

MAUCHLINE,J.& T.NEMOTO, 1977. Integumental sensilla of diagnostic value in euphausiids. Journal of the Oceanographic Society of Japan, 33:283-289.

MAYR,E., 1963. Animal Species and Evolution. Havard University Press, Cambridge, Mass., U.S.A. 797pp.

MAYR,E., 1969. Introduction: the role of sytematics in biology. In Systematic Biology. Proceedings of the International Conference on Systematic Biology, University of Michigan, June 14-16, 1967. Publ.1692, National Academy of Sciences, Washington, D.C., pp 4-15.

MAYR,E., 1979. Modes of speciation. Systematic Zoology, 27(4):478-482.

MEYER-ROCHOW, V.B., 1981. Note on the cuticular morphology in the terrestrial amphipod Orchestia sp. (Crustacea). Zoologischer Anzeiger, 207(1-2):74-77.

MOLNAR,P., T.ATWATER, J.MAMMERICKX and S.M.SMITH, 1975. Magnetic anomalies, bathymetry, and the tectonic evolution of the South Pacific since the late Cretaceous. Geophysical Journal of the Royal Astronomical Society, 40(3):383-420.

MORINO,H., 1972, Studies on the Talitridae (Amphipoda, Crustacea): 1 Taxonomy of Talorchestia and Orchestoidea. Publication of Seto Marine Laboratory, 21(1):43-65.

MORINO,H., 1975, Studies on the Talitridae (Amphipoda, Crustacea) in Japan: II. Taxonomy of sea-shore Orchestia, with notes on the habitats of Japanese sea-shore Talitrids. Publication of Seto Marine Laboratory, 22(1-4):171-193.

MORINO,H., 1978. Studies on the Talitridae (Amphipoda, Crustacea) in Japan. III. Life history and breeding activity of Orchestia platensis Kroyer. Publication of Seto Marine Laboratory, 24:245-267.

NELSON,G.& N.PLATNICK, 1981. Systematics and Biogeography, Cladistics and Vicariance. Columbia University Press, New York, 567pp.

NELSON,G.& D.E.ROSEN, 1981. Vicariance Biogeography: A Critique. Columbia University Press, New York, 593pp.

NEW ZEALAND DEPARTMENT OF LANDS AND SURVEY, 1968. Gazetter of New Zealand Place Names. A.R.Shearer, Government Printer, Wellington, 575pp.

NIE,N.H.,C.H.HULL,J.K.JENKINS,K.STEINBRENNER & D.H.BENT, 1975. SPSS: Statistical Package for the Social Sciences. 2nd ed., McGraw-Hill, New York, 675pp.

PATTERSON,C., 1982. Morphological characters and homology. In Problems of Phylogenetic Reconstruction. K.A.JJoysey & A.E.Friday (eds.), Academic Press, London and New York. 442 pp.

NUR,A.& Z.BEN-AVRAHAM, 1981. Lost Pacifica continent; a mobilistic speculation. In Vicariance Biogeography; A Critique. G.Nelson & D.E.Rosen (eds.), Columbia University Press, New York. pp 341-358.

PLATNICK,N.T.& G.NELSON, 1978. A method of analysis for historical biogeography. Systematic Zoology, 27(1):1-16.

REED,A.W.& A.E.BROUGHAM, 1978. The Concise Maori Handbook. A.H.& A.W.Reed, Wellington, 587pp.

RICHARDSON,A.M.M., 1980. Notes on the occurrence of Talitroides dorrieni Crustacea Amphipoda Talitridae in Southwest England UK. Journal of Natural History, 14(6):751-758.

SCHMALFUSS,H. 1976. Constructional morphology of cuticular structures in crustaceans. Neues Jahrbuch fur Mineralogie, Geologie und Palaontology: Abhandlungen, 157(1-2):155-159.

SCHMALFUSS,H., 1978. Ligia simoni: A model for the evolution of terrestrial isopods. Stuttgarter beitrage zur naturkunde, Ser.A (Biol.), 317:1-5.

SCHMALFUSS,H., 1978. Morphology and function of cuticular microscales and corresponding structures in terrestrial isopods (Crust., Isop., Oniscoidea). Zoomorphologie 91(3):263-274.

SEGERSTRALE,S.G., 1954. The freshwater amphipods, Gammarus pulex (L.) and Gammarus lacustris G.O.Sars, in Denmark and Fennoscandia - a contribution to the late- and post-glacial immigration history of the aquatic fauna of Northern Europe. Finska vetenskaps-societeten, Helsingors. Acta Societatis scientiarum fennicae. Opera biologica, 15(1):1-91.

SHOEMAKER,C.R., 1935. A new species of amphipod from Mt.Kinabalu, North Borneo. Bulletin of the Raffles Museum, Singapore, 135(10):64-67.

SHOEMAKER,C.R., 1942. Amphipod Crustaceans collected on the Presidential cruise of 1938. Smithsonian Miscellaneous Collection, 101, Art.11 (3677);1-52.

SHYAMASUNDARI,K.& K.HANUMANTHA RAO, 1974. The occurrence of mucus glands in the appendages of Talorchestia martensii (Weber) and Orchestia platensis Kroyer (Crustacea, Amphipoda). Current Science, 43(4):122-123.

SNEDECOR,G.W.& W.G.COCHRAN, 1967. Statistical Methods. 6th Ed. Iowa State University Press, Ames, Iowa. 593pp.

STEBBING,T.R.R., 1899. Amphipoda from the Copenhagen Museum and other sources. Part II. Transactions of the Linnean Society of London, Zoology, Series 2, 7(8):395-432.

STEBBING,T.R.R., 1906. Amphipoda Gammaridea. Das Tierreich, Vol.21, 806pp.

STEPHENSEN,K., 1935. Indo-Pacific terrestrial Talitridae. B.P.Bishop Museum Occasional Papers, 10(23):1-20.

STEPHENSEN,K., 1938. Amphipoda, Tanaidacea und Pycnogonida. Senckenbergiana, 20(3/4):236-264.

SOLEM,A.& F.M.CLIMO, 1981. Sympatric species diversity of New Zealand land snails. New Zealand Journal of Zoology, 8:453-485.

STOUT,J.D., 1973. Soil Ecology. In The Natural History of New Zealand, An Ecological Survey, Gordon R.William (ed.), A.H.& A.W.Reed, Wellington, pp 131-154.

SUGGATE,R.P., 1976. Geology. In New Zealand Atlas. I.Wards (ed.). A.R.Shearer, Government Printer, Wellington, 291pp.

SUGGATE,R.P., 1978. The geology of New Zealand. 2 volumes. E.C.Keating, Government Printer, Wellington.

TEDFORD,R.H., 1981. Discussion to paper by A.Nur & Z.Ben-Avraham. In Vicariance Biogeography; A Critique. G.Nelson & D.E.Rosen (eds.), Columbia University Press, New York, 593 pp.

THOMSON,G.M., 1881. Recent additions to, and notes on, New Zealand Crustacea. Transactions of the New Zealand Institute., 13:204-221.

THOMSON,G.M., 1884. Descriptions of new Crustaceans. Transactions of the New Zealand Institute, 16:234-240.

THOMSON,G.M., 1899. Synonymy of the New Zealand Orchestidae. Transactions of the New Zealand Institute, 31:197-207.

THOMSON,G.M.& C.CHILTON, 1886. Critical list of the Crustacea Malacostraca of New Zealand. Transactions of the New Zealand Institute, 18:141-159.

VADER,W., 1972. Terrestrial Amphipoda collected in greenhouses in the Netherlands. Zoologische bijdragen, (13):32-36.

VAN ANDEL,T.H., 1976. An eclectic overview of plate tectonics, paleogeography, and paleoceanography. In Historical Biogeography, Plate tectonics and the Changing Environment. Proceedings of the Thirty-seventh Annual Biology Colloquium and Selected Papers. Jane Gray & A.J.Boucot (eds.). Oregon State University Press, pp 9-26.

VINCENT,J.F.V., 1982. Structural Biomaterials. MacMillan, London, 207pp.

WAGSTAFFE,R.& J.H.FIDLER, 1955. The preservation of Natural History Specimens. Vol.I. Invertebrates. H.F.& G.Witherby, London, 205pp.

WARHAM,J.,B.R.KEELEY & G.J.WILSON, 1977. Breeding of the mottled petrel. The Auk, 94(1):1-17.

WEISSEL,J.K.,D.E.HAYES & E.M.HERRON, 1977. Plate tectonics synthesis: The displacements between Australia, New Zealand, and Antarctica since the Cretaceous. Marine Geology, 25(1-3):231-277.

WHITE,M.J.D., 1978. Modes of Speciation. W.H.Freeman, San Francisco, 455pp.

WILDISH,D.J., 1979. Reproductive consequences of the terrestrial habit in Orchestia (Crustacea: Amphipoda). International Journal of Invertebrate Reproduction, 1:9-20.